

AN INTERDISCIPLINARY APPROACH TO RESTORATION: HAWAIIAN SEABIRDS AS  
A CASE STUDY

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## ABSTRACT

Seabirds are experiencing dramatic declines in both their ranges and populations, resulting in decreases in ecosystem services they provide. Seabird breeding islands were historically rodent and mostly predator free, allowing seabirds to nest colonially and deposit large quantities of guano and other organic material. On average seabirds can increase inputs of nitrogen (N) and phosphorus, the two most common limiting and co-limiting nutrients to primary productivity, by 100 and 400% respectively. The goal of this research was to improve understanding of the impacts of decreased seabird numbers on ecosystems and the challenges to restoration. To address how losses of seabirds affect island ecosystems, the objectives of this research were to gain a better understanding of the historic role that seabirds played in the past, how that compares to current nutrient deposition, and how current efforts to restore seabird populations affect the native ecosystems. Using historical data and species habitat density models, I determined that seabird deposition of nitrogen into Hawaiian ecosystems was likely three – four orders of magnitude higher than it is today. During the pre-human era, seabirds could have deposited 1,460 – 5,290 kg of N ha<sup>-1</sup> year<sup>-1</sup>. Based on current population estimates, and historic habitat, seabirds are currently contributing 0.535 kg of N ha<sup>-1</sup> year<sup>-1</sup>. To address the current impact of seabirds on montane systems in Hawai‘i, I measured inorganic labile soil nutrients  $\delta^{15}\text{N}$  of seabird and non-seabird plots to determine marine-sourced N in the soil and foliage of two dominant plants. More  $\text{NH}_4^+$  was found in the soil of seabird colonies than non-seabird colonies, and 28% of foliar N in the dominant tree and 17% of foliar N in a dominant understory plant, were from marine source. However, plant species composition was similar between seabird and non-seabird areas, despite differences in nutrient availability. Finally, I determined that costs of management actions vary widely depending on terrain and accessibility of the site,

but all actions have positive ecosystem services benefits. As restoration of native ecosystems continue to be a priority, understanding the role seabirds played in the past and how they currently contribute to the ecosystem are critical for effective restoration efforts.

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## CHAPTER 1. INTRODUCTION

Seabird populations are declining globally and of the 346 seabird species currently recognized, 102 are threatened or endangered and five are considered extinct (Jones 2010, Croxall et al. 2012, Gaskin and Rayner 2013). Threats to seabirds include introduced predators, habitat loss, bycatch in long-line fisheries, reduction of prey items in the ocean, plastic ingestion, and pollution (Ratcliffe et al. 2009, Bellingham et al. 2010, Croxall et al. 2012, Hatfield et al. 2012). Seabirds play important roles in many ecosystems, as seabirds are lost, so too are their services. Seabirds are most well-known for transporting nutrients from marine to terrestrial environments (Bancroft et al. 2005, Fukami et al. 2006, Whelan et al. 2008, Durrett et al. 2014), and physically changing the environment they nest in by burrowing, trampling and uprooting plants, depositing seeds from distant communities, and depositing large amounts of organic material (Wainright et al. 1998, Mulder and Keall 2001, Wait et al. 2005, Gagnon et al. 2013). Cultural and spiritual connections are also important (KERSP n.d., Chan et al. 2012).

While islands hold a large percentage of global biodiversity, they also experience high extinction rates and are sensitive to introduced species (Sadler et al. 2007, Glen et al. 2013). Over 90% of islands have been invaded by rats (*Rattus* spp.) and many of these have also been invaded by cats (*Felis catus*) (Jones et al. 2008, Croxall et al. 2012). Rats and cats are the largest threats to seabirds on their nesting grounds (Croxall et al. 2012, Spatz et al. 2014, Jones et al. 2016) and seabirds are not equipped to protect themselves and their eggs from predators. Historically seabirds have thrived on predator-free islands (Maron et al. 2006, Bellingham et al. 2010, Buxton et al. 2014). Seabird populations have plummeted as humans have intentionally and accidentally introduced predators to these islands. Seabirds may nest on a slope on the ground, in trees, in burrows, or crevasses. Most nesting strategies of seabirds leave them



vulnerable to many possible predators. Invasive ungulates can also cause damage to burrows from trampling (Towns et al. 2009; Fukami et al. 2006; Ratcliffe et al. 2009). Loss of seabirds from islands not only deals a blow to biodiversity, but has far reaching impact throughout the ecosystems (Jones 2010).

Many terrestrial ecosystems have evolved with seabirds over millennia, and seabirds have historically provided an important source of nutrients from the marine environment (Maron et al. 2006, Jones 2010, Leblans et al. 2014, Doughty et al. 2015). Thus, when seabird populations decline these terrestrial ecosystems lose a large source of nutrients (Ellis 2005). Seabirds feed on fish, squid, and other organisms from the ocean that are composed of large amounts of nitrogen (N) and phosphorus (P), which translates into guano that is high in N and P. Average guano composition for seabirds worldwide is approximately 60% water, 7.3% N and 1.5% P. For pelagic seabirds (e.g. petrels, shearwater, albatross), N content of guano ranges from 14.9–28.6%. In the case of burrowing seabirds (e.g., petrels and shearwaters) it has been estimated that may bring in 100 times more N and up to 400 times more P than the annual input from rainwater or other passive deposition (Anderson et al. 2008, Mulder et al. 2011).

The loss of nutrient transfers from marine to terrestrial ecosystems due to the global reduction of seabird populations may have significant effects on ecosystem productivity (Mulder and Keall 2001; Young et al. 2010, 2011). N and P are the main limiting and often co-limiting macronutrients to primary productivity (Menge et al. 2012; Elser et al. 2007; Posada and Schuur 2011). Allochthonous nutrient subsidies have also been shown to affect the entire food web in recipient communities (Ellis 2005; Mellbrand et al. 2011; Caut et al. 2012; Young et al. 2010). High seabird densities impact nutrient runoff into the marine environment and increase density of emerging insects (Kolb et al. 2010). Marine sourced N have been found in plants,

invertebrates and lizards in studies in New Zealand (Markwell and Daugherty 2003). Forest nesting petrel colonies in New Zealand were found to provide foraging opportunities to forest birds by enriching invertebrates as well as plants (Hawke and Holdaway 2009). Nutrient subsidies in arid communities have resulted in increases in plant productivity as well as invertebrate size and fecundity (Wait et al. 2005). However, ecologists do not fully understand what the loss of these nutrients means to different ecosystems, although ecosystem functionality has returned when seabirds are restored to historical seabird islands (Mulder et al. 2009, Bellingham et al. 2010, Towns et al. 2016).

The loss of biodiversity and the loss of services are a concern for many agencies and organizations worldwide (Rauzon 2007, Fischer et al. 2007, Croxall et al. 2012). As coastal ecosystems around the world experience similar seabird losses they are also losing the ecosystem services that seabirds traditionally provided (Chown et al. 1998, Lewison and Crowder 2003, Gaston et al. 2003). In response to these losses, a great deal of time and money have been dedicated to seabird restoration.

In Hawai‘i the same story of seabird loss is playing out. Many seabird species have been extirpated from the Hawaiian Islands and one has gone extinct (*Pterodroma jugabilis*) (Olson and James 1991, 1994, Burney et al. 2001, Hearty et al. 2005, Welch et al. 2012). All nesting seabird species have decreased in population number and geographic range size, and only seven pelagic species continue to breed in the main Hawaiian (Munro 1955; Brandt et al. 1995; Harrison 1990; Duffy 2010; Olson and James 1991; Welch et al. 2012). For instance, the Federally endangered and endemic Newell’s Shearwater populations declined 95%, the Hawaiian Petrel has declined by 78% from 1993 to 2013 (Raine et al. 2017) and Tristram's storm

petrel (*Oceanodroma tristrami*) no longer breeds in the main Hawaiian islands (McClelland et al. 2008).

Seabird restoration in Hawai‘i has been ongoing for at least 50 years by non-profit organizations and government agencies, but much more time and money have been invested in the last ten years as the plight of some of the endemic seabirds has become more dire (Griesemer and Holmes 2011). Recently, for-profit entities such as wind and electric companies have funded projects for seabird restoration to mitigate losses that their operations may cause (Serivce 1982, Rosegg and Kaluhiwa 2011). The most common action involved in seabird restoration is invasive species control, typically of nonnative predators (Jones et al. 2008, Jones 2010, Glen et al. 2013, VanderWerf et al. 2014). Total eradication of invasive species has been successful on some uninhabited islands (Bellingham et al. 2010, Aguirre-Muñoz et al. 2011, Towns et al. 2016), but may be nearly impossible on large populated islands like the main Hawaiian Islands (Glen et al. 2013). Restoration projects typically have a monitoring program to both measure changes in seabird population numbers, and to track ingress of invasive animals (Rauzon 2007, Buxton and Jones 2012, Glen et al. 2013). All of these actions have costs associated with them that vary depending on the site location and project goals (Holmes et al. 2016). To make the best decisions for seabird restoration it is important for managers and decision makers to understand the costs and benefits that possible actions incur.

To address the problems associated with seabird loss, I sought to understand seabirds’ role in Hawaiian ecosystems. Specifically, I took a past, present, and future approach to understand seabirds’ role in ecosystems in the past, what they may contribute today, and how seabird restoration projects contribute to Hawai‘i today and into the future. Specifically, I sought to address three main research questions. First, how much N could seabirds have contributed in a

pre-human past and how does that compare to the quantities of N that they may be contributing to terrestrial ecosystems currently? Second, do montane nesting seabirds currently impact the ecosystems where they nest? Third, what are the costs and ecosystem services benefits associated with seabirds' restoration actions?

Ecosystem functionality is dependent on robust biodiversity (Soliveres et al. 2016). Loss of biodiversity is a complicated issue affecting most parts of the world with potentially dire consequences (Doherty et al. 2016). Being able to put the loss of biodiversity into context is important to determining potential restoration actions. The research presented here addresses the loss of seabirds in the main Hawaiian Islands, what ecosystem services are lost with seabird decline as well as what ecosystem services improve with seabird restoration. While these studies took place in Hawai'i, they are applicable and valid for many areas globally that are experiencing loss of biodiversity. Sustainable restoration of seabirds, as well as other organisms and ecosystems, is complex and inherently interdisciplinary. The concepts and challenges encountered here are indicative of many concepts and challenges encountered in restoration work more broadly. In as much, it is my hope that this research may inform the work of others around the world.

## **CHAPTER 2: PAST AND PRESENT INFLUENCE OF SEABIRDS' ON NATIVE HAWAIIAN ECOSYSTEMS**

### **Abstract**

Seabirds have long been integral to coastal ecosystems through such functions as moving nutrients from marine to terrestrial ecosystems. While integral to ecosystems, seabird populations are in decline throughout the world. Given these declines, the goal of this research was to understand how much nutrient deposition may have been lost with seabird range contractions and population decline. To determine changes in nutrient deposition rates I used historical accounts and sub-fossil evidence combined with current knowledge of seabird species nesting requirements across the Hawaiian Islands and developed a habitat-area probability model to estimate potential pre-human nesting habitat. I calculated N deposition rates for 10 pelagic seabird species, corrected for different body masses, and used seabird nesting density estimates to determine how much N may have been deposited under historic high- and low-density seabird population scenarios. Potential breeding habitat across all the main Hawaiian Islands in the pre-human environment was ~283,700 ha. During the pre-human era, pelagic seabird could have deposited between 1,460 and 5,290 kg of N ha<sup>-1</sup> year<sup>-1</sup>. If the current population of seabirds was distributed over historic range, then density of birds would fall to 0.29 kg of N ha<sup>-1</sup> year<sup>-1</sup>, yielding a deposition rate of 0.535 kg of N ha<sup>-1</sup> year<sup>-1</sup>. Thus, Hawai'i has experienced a 99.98% loss in N provisioning since the arrival of humans. As a result, seabirds likely had a large impact on these ecosystems and the organisms that inhabit them. Thus, restoring seabird habitat and population size is a key aspect of restoring Hawai'i's ecosystems.

## Introduction

Seabirds contribute to the transportation of millions of kilograms of nitrogen (N), phosphorus (P), and other nutrients from marine to terrestrial ecosystems (Doughty et al. 2015). However, seabirds have declined by as much as 69% between 1950 and 2010 around the world, with pelagic seabirds suffering the highest rates of decline (Paleczny et al. 2015), resulting in a drop of global nutrient deposition to 6.3 million kg km<sup>2</sup> year<sup>-1</sup> (Doughty et al. 2015). Deposition of organic material via seabirds including guano, dropped food, carcasses, and egg shells is the largest input of nutrients to many ecosystems (Anderson and Polis 1999, Wait et al. 2005). Seabirds feed on fish, squid, and other organisms from the ocean as reflected in the nutrient portfolio of their guano (Blais et al. 2005, Mulder et al. 2011). Specifically, average guano composition for seabirds worldwide is approximately 60% water, 7.3% N, and 1.5% P. However, for pelagic seabirds, nutrient composition of guano is even higher, with N ranging from 14.9–28.6% (Mulder et al. 2011). Nesting seabirds also deposit nutrient-rich organic material in the form of dropped prey items, abandoned eggs, bird carcasses, and feathers (Mulder et al. 2011, Leblans et al. 2014).

In the past, Hawai‘i was home to at least 11 pelagic seabird (Procellariiforms) species (Harrison 1990, el Hoyo et al. 1992). Historical accounts and sub-fossil remains indicate that more species of seabirds nested on the Hawaiian Islands in much higher densities in the past than today (James 1990, 1995, Burney et al. 2001). Currently seven of the 11 seabird species breed in the main Hawaiian Islands with most being greatly reduced in number and geographic distribution (Ferber et al. 1983, Harrison 1990, Bond et al. 2010). For instance, the band-rumped petrel population is estimated at 240 breeding pairs and Bulwer’s petrel is estimated 500–1000 breeding pairs (KERSP n.d., Munro 1955, Harrison 1990, Brandt et al. 1995, Duffy 2010, Young

et al. 2013) (Table 2.1). Seabird population declines are primarily a result of introduced predators (Rauzon 2007), loss of nesting habitat to development, trampling and rooting by nonnative ungulates, fallout from collisions with power lines and man-made structures (Erickson and Johnson 2005), and fallout from light pollution (Day et al. 2003, Reed et al. 2012).

At present seabirds in Hawai‘i nest in a subset of their historic range (Ferfer et al. 1983). For instance, the Hawaiian Petrel (*Pterodroma sandwichensis*) is the most widely ranging species across the main islands and is found in xeric pāhoehoe lava fields, densely vegetated wet forest, and dry alpine and sup-alpine shrubland on Hawai‘i, Kaua‘i, Maui and Lana‘i (VanZandt et al. 2014), but it historically nested on Moloka‘i and O‘ahu as well and breeding sites located from the mountains to the coast (Richardson and Woodside 1954, Olson and James 1991, Milberg and Tyrberg 1993). Aside from uncertainty about the marked decreases in habitat is the problem with historical reconstruction of pre-settlement vegetation in Hawai‘i. While many native species and ecosystems continue to persist, the exact composition of the systems remains unknown.

The large reduction in seabird populations mean that seabird nutrient deposition also has decreased. Nutrient deposition is important in Hawaiian ecosystems because primary production in tropical montane wet forests has been shown to be limited by N and/or P, depending on substrate age. In particular, older substrates are limited by P, younger substrates are limited by N, and mid aged substrates are co-limited by both N and P (Walker and Syers 1976, Vitousek and Farrington 1997). Because Hawai‘i is a high rainfall system, much N and P is lost through leaching and erosion (Posada and Schuur 2011). The primary non-anthropogenic sources of N are from biological-fixation of atmospheric N<sub>2</sub>, while P is typically gained from rock weathering, and in older ecosystems, wet and dry deposition (Kurtz et al. 2001). Seabirds are one of only a

few sources of allochthonous N and P (Wainright et al. 1998), and are important to many islands systems, including Hawai‘i (Kremen 2005, Sekercioglu 2006, Wright et al. 2010).

Nesting seabirds may increase N and P inputs by 100 to 400 times compared to terrestrial systems without seabirds (Mulder et al. 2011). Subsequently, the potential loss of multiple seabird colonies, and even entire species from the islands, represents a dramatic loss of nutrients compared to pre-contact Hawai‘i (Wait et al. 2005, Mulder et al. 2011, Caut et al. 2012). To understand the ecosystem consequences of seabird loss, it is necessary to know how much N pelagic seabirds might have brought to the ecosystems where they nested in the pre-human past.

Given the large declines in seabird numbers, the goal of this research was to understand how much nutrient deposition may have been lost with seabird range contractions and population decline since presettlement. To address this goal, I had two main objectives: 1) quantify the possible rates of N deposition by seabirds to the main Hawaiian Islands prior to human colonization; and, 2) understand that deposition in the context of current seabird nutrient deposition. The comparison between pre-human and current N deposition elucidates how much allochthonous nutrients the island ecosystems have lost in the last 1,000 years.

## **Methods**

To address my objectives, I developed a model to calculate potential nutrient input of the historic pelagic seabird community on the main Hawaiian Islands (Hawai‘i, Maui, Kaho‘olawe, Lāna‘i, Moloka‘i, O‘ahu, Ni‘ihau and Kaua‘i). Ideally spatially explicit habitat suitability models include presence and absence data of target species across the habitat with sufficient sampling to statistically infer suitability across multiple spatial variables. However, historic presence/absence seabird data does not exist. Hence, seabirds historically nesting on the main Hawaiian Islands



were identified by literature review of papers discussing early bird surveys, and sub-fossils discovered in caves, middens, and sinkholes in Hawai‘i (Olson and James 1982, 1991, Burney et al. 2001, Hearty et al. 2005, Langenwalter and James 2015) resulting in 10 species with enough information available to develop historic potential habitat maps (Table 2.1). The bird species weight, breeding season, and habitat requirements were derived from published species reports where available or from published research on closely related species (Del Hoyo et al. 1996, Higgins and Davies 1996, Young et al. 2009, Griesemer and Holmes 2011, Mcfarland and Raine 2012, Joyce 2013, Troy et al. 2014, 2016, Leblans et al. 2014, VanderWerf et al. 2014). In terms of abiotic habitat data, elevation, basic age of lava flows, and slope were all identified as important (Troy et al. 2014, Vorsino 2017). Given all available data a habitat suitability model that could determine different levels of habitat quality was not possible to develop for individual species nor was a statistically driven population-density model. However, a basic wildlife-habitat relationship model was possible.

To develop the basic wildlife-habitat relationship I determined nesting habitat parameters for each of the seabirds considered in this study (Table 2.1). Specifically, elevation, slope, and distance from ridgelines explained 31% of variance for Cook’s petrel (*Pterodroma cookie*) burrow location (Rayner et al. 2007), and slope was one of the top three habitat predictors for Newell’s Shearwater nesting habitat in a recent habitat suitability modeling paper (Troy et al. 2014). Similarly, I used elevation, slope, substrate age, and distance from coast to determine nesting area categories. With these criteria, I created the broad categories of Coast, Lava, and Cliff. The Coast category consists of areas than are within 1 km of the coastline, as many seabirds are found nesting from the coast to 500–1,000 m (Rodewald 2015, L. Young pers. comm. 2016, and A. Raine, pers. comm. 2016). The Lava category includes areas with a young

substrate in the dry to mesic moisture classes following Price et al. (2012). The area that was classified as Lava was then divided by two to account for the discrepancy between a‘a and pahoehoe lava. Pahoehoe lava is characterized by smooth surface, while a‘a lava is rough, jagged, and fragmented. Seabirds are known to nest in pahoehoe lava, but not in a‘a lava. While these two lava types may not be distributed in equal proportions across the landscape, there is no known study defining proportion of the landscape covered by a‘a and pahoehoe lava. I therefore assumed 50% a‘a and 50% pahoehoe lava (pers. comm. K. Hon, UH Hilo). I calculated the Cliff category to encompass seabird habitat in burrows and crevasses on steep slopes. Based on existing research (Rayner et al. 2007, Troy et al. 2014, VanZandt et al. 2014) I calculated  $> 45^\circ$  slope on a 30 m Digital Elevation Model (USGS DEM) to estimate the Cliff category. Some areas fell into more than one of these three categories. For example, in some areas near the coast there are also cliffs. In this case, I combined the two overlapping categories to make an additional category to avoid double counting. In the example of a coastal cliff there would be three categories: Coast, Cliff, and Coast + Cliff, which are all mutually exclusive. I then assigned each bird species into one or more of these categories by considering current habitat requirements, places where the birds have been found in the past (including sub-fossil localities), and comparisons to closely related species (Olson and James 1982, Brooke 1995, Gallo-Reynoso and Figuero-Carranza 1996, Keitt et al. 2003, Judge and Hu 2007, McFarland and Raine 2012). All habitat mapping was conducted in GIS (ARCGIS 10, UTM Zone 4, NAD83).

Seabird nesting densities were estimated from published literature and expert opinion (Smith et al. 2001, Cuthbert and Davis 2002, Keitt et al. 2003, Bourgeois and Vidal 2007, Rayner et al. 2007, Young et al. 2009, Gaskin and Rayner 2013, L. Young pers. comm. 2016, J. Penniman pers. comm. 2015)). I used high- and low-density estimates for each species (Table

2.1) to determine how many birds could have nested on the islands (Grant et al. 1981, Keitt et al. 2003, Troy et al. 2014, VanZandt et al. 2014). Many seabirds are colonial nesters and will nest in a clumped pattern with conspecifics or other species of seabirds (Coulson 2001). However, due to competitive exclusion, the nesting density is not additive so in areas where potential nesting habitat overlapped I averaged the nesting density of the birds sharing habitat, and calculated an average of their N deposition potential (Oro et al. 2009). To account for microhabitat selection and clumped nature of seabird nesting, I multiplied the nesting density across all available habitat by 0.5.

Because no studies have been conducted indicating the amount of food consumed or the amount of excreta produced per day for any of the 10 seabirds evaluated, I estimated the amount of food ingested and excrement produced based on values for other seabirds found in the literature and adjusted that to fit the seabirds in this study using an allometric equation (Schneider 2002). Specifically, daily intake was by species was calculated as:

$$\text{Intake(g)} = \text{Mass(g)}^{0.72}$$

For each species, I used the published average body mass to estimate daily food intake assuming birds are in homeostasis (Table 2.2). For example, the average mass for Newell's Shearwater is 0.384 kg (Ainley et al. 1997), which translates to 72.6 g of marine based food day<sup>-1</sup>. The daily amount of food consumed was divided by 10.4 to calculate the guano production, based on a metabolic study of dovebies (Gabrielsen et al. 1991). I determined daily guano production for the 10 seabirds. Mulder et al. (2011) found that guano composition ranged from 14.9–28.6% N for pelagic seabird guano, while I found 19.9–33.5% N in guano with a mean of 28.9% N for Newell's Shearwater and Hawaiian Petrel in a study on Kauai (Rowe et al. 2017). Therefore, I used 28% N composition for the calculation of N composition in guano. Using the same

Newell's Shearwater example, one Newell's Shearwater would consume 72.6 g of food day<sup>-1</sup> and produce 6.98 g of guano day<sup>-1</sup> which would be approximately 1.95 g of N day<sup>-1</sup>. For each seabird, the length of the breeding season measured in days, was multiplied by the amount of N deposited per day and divided by two to adjust for one bird of each pair staying at the nest while the other forages. This quantity of N deposited per breeding pair was then multiplied by the number of breeding pairs that could have nested in the available habitat per island (high- and low-density estimates). The total kg N per year for each habitat class was then calculated for each island (Table 2.3). For current N deposition, I used current population estimates for the pelagic seabirds nesting in Hawai'i (Pyle and Pyle 2009) to estimate how much N they may be depositing on an annual basis. This number is representative of the entire breeding population of each species in Hawai'i and no effort was made to determine suitable habitat. For further discussion on current seabird habitats see (Troy et al. 2014).

## **Results**

Historic available nesting habitat ranged from 4,970 ha on Kaho'olawe to 155,500 ha on Hawai'i (Table 2.3). Deposition rates ranged from 828–3,811 kg of N ha<sup>-1</sup> year<sup>-1</sup> on Hawai'i Island to 2,987–9,916 kg of N ha<sup>-1</sup> year<sup>-1</sup> on Ni'ihau (Table 2.3). Total potential habitat across all islands was 283,750 ha, which would result in 460,374,908–1,675,609,010 kg of N year<sup>-1</sup>. Coast habitat received the highest rate of deposition (3,010–10,040 kg of N ha<sup>-1</sup> year<sup>-1</sup>) while Lava received the lowest (370–2,570 kg of N ha<sup>-1</sup> year<sup>-1</sup>) (Table 2.4). At current seabird population levels (Table 2.1), seabirds may bring in 151,720 kg of N kg year<sup>-1</sup> to the main Hawaiian Islands. This represents a 3.8 magnitude loss of N deposition to Hawaiian ecosystems.

Hawaiian petrels had much more available habitat in the pre-human past than currently, with a substantial decrease over time in low elevation colonies on pahoe lava of Hawai'i Island. However, even though Hawaiian petrel range covered more area, Laysan albatross may have contributed more N to the ecosystem due to its larger body size. Newell's Shearwater also had more land available for breeding than they currently use, most pronounced along ridge lines on Kaua'i and O'ahu. Coast nesting habitat was the largest habitat category for all islands except Hawai'i. On Hawai'i Island, Lava constituted the largest habitat category (120,800 ha). Hawai'i Island had much more available habitat for nesting seabirds, especially in the Lava (120,800 ha), Coast (21,200 ha), and Coast + Lava (10,100 ha) categories, than is currently utilized (Figure 2.3). Maui was estimated to have 7,000 ha available of Cliff habitat and 19,100 ha of Coast habitat. O'ahu's potential cliff habitat encompassed 3,300 ha while potential coastal habitat covered 32,600 ha (Figure 2.3). Kaua'i has a large amount of potential cliff nesting habitat (7,100 ha) as well as coastal (18,200 ha) (Figure 2.3). Currently, nesting seabird populations are restricted to scattered coastal nesting sites and a few cliff nesting populations

## **Discussion**

Hawaiian ecosystems have lost 99.98% of seabird deposition of N since the arrival of humans. This decrease in deposition rates is a result of both reduction in species abundances and suitable habitat. The difference between deposition potential in the habitat categories is related to the birds that typically nest there. Small birds that produce little guano, like Hawaiian Petrel nest in Lava, and larger seabirds like albatross that produce much more guano per bird, nest in Coast. Islands with large Coast areas have lost the largest amount of nutrients as these are the areas with the highest deposition rate and are the most vulnerable to predation and development. Large

areas in all habitat categories have been lost to seabirds and all birds have experience range contraction.

For example, the Hawaiian petrel currently nests in high elevation ecosystems in Hawai‘i, but it is known that they nested from the coast to the mountains in the past (Simons 1984, Wiley et al. 2013, VanZandt et al. 2014). When the Hawaiian petrel’s habitat of Lava and Cliffs is expanded into lower elevation areas, the amount of breeding habitat available to the petrels that is not currently utilized on Hawai‘i Island is large. Newell’s shearwater may have always preferred high elevation nesting spots and may not have had large populations, but they too have room to expand on the main islands in the absence of predators.

One of the main reason that so much more breeding area was available for nesting habitat in the past is due to invasive mammals (Jones et al. 2008). Many seabirds need sandy soil to nest in and many of them prefer low native vegetation (Ellis 2005). Some pelagic seabirds dig burrows in the sand and some nest directly on the sand in what is referred to as a scrape. These types of nests are vulnerable to nonnative cats, dogs, rats, mice, mongoose, and feral pigs. In this model, in the pre-human past these threats were all removed. While seabirds may have faced predation from land crabs (Paulay and Starmer 2011) and possibly Hawaiian eagles (Olson and James 1982, Hailer et al. 2015), the pressure would have been much lower than current pressure from invasive mammals (Jones et al. 2008, Buxton et al. 2014).

When seabirds are restored to island habitats through passive or active restoration, ecosystem function can also be restored (Jones 2010, Aguirre-Muñoz et al. 2011, Kappes and Jones 2014, Towns et al. 2016). Significant work in the last 30 years to eradicate invasive mammals and to restore seabirds have led to several examples of how islands and ecosystems can respond to the restoration of seabirds (Martínez-Gómez and Jacobsen 2004). On the

Korapuki Islands, New Zealand, pacific rats (*R. exulans*) and rabbits (*Oryctolagus cuniculus*) were removed and seabirds and tuatara (endemic lizard) have returned, resulting in the re-establishment of an intricate seabird-reptile-invertebrate-plant connections (Towns and Atkinson 2004, Towns et al. 2016). In the Aleutian Islands, when foxes were removed seabirds responded with a five-fold population increase within ten years, which increased nutrient subsidies to a nutrient poor ecosystem (Rauzon 2007).

The wildlife-habitat model described here is coarse due to a paucity of data from the past and is based on several assumptions. To estimate food intake for each seabird species, birds were assumed to be in homeostasis, and intake rate was based on an allometric equation. Second, because many seabirds have discontinuous habitat selection across all available habitat (Brandt et al. 1995, Rayner et al. 2007) I attempted to capture unevenness by calculating high and low estimates of nesting densities and reducing the density across the island to reflect clumping. While predictive model estimates can give more accurate results than simple or habitat models (Rayner et al. 2007), some of the accuracy and strength of these models comes from the input of more precise data than is available for the calculations in this research. I generalized the nesting requirements of the seabirds into broad categories which may lump some birds into elevations where they may not nest, and may leave some birds out of microhabitat that may be available to them. While this may result in over estimation in some cases and under estimation in others, there was no systematic bias. There may be other limiting factors to seabird population numbers besides available nesting habitat, in which case this would provide an over estimate of N deposition. There may also be predator-prey interactions that are not understood currently, which could allow for an over estimation of N deposition by seabirds.

The decline of seabird populations and the subsequent loss of nutrient deposition has implications for the native ecosystems where these birds once nested. In Hawai‘i, montane nesting seabirds are declining precipitously and some coastal seabirds have been extirpated from the main islands altogether, while the remaining species are in much reduced numbers. Nitrogen and other nutrients found in seabird guano are vital to ecosystem function and productivity (Schlesinger 1997). The effects of alterations in nutrient deposition are evident throughout the food web (Stapp et al. 1999, Wiley et al. 2013, Vizzini et al. 2016), therefore the loss of these nutrients likely has ecosystem wide effects. While no ecosystem is static and the nutrient deposition estimates presented here are coarse, there is little doubt that seabirds of the pre-human era delivered much more nutrients than they do today.

Land managers can work together with seabird restoration project managers to bring seabirds back to areas where they once nested. Of utmost importance to facilitate this change is the exclusion of rodent and other mammalian predators (Rauzon 2007, Doherty et al. 2016, Jones et al. 2016). Eradication of rodents and other predators like cats and mongoose is ideal, but in many situations where the island or land area is inhabited, eradication is virtually impossible (Myers et al. 2000). Eradication, or at least exclusion of predators has far reaching positive consequences throughout the ecosystem (Jones et al. 2016). Other action can be taken to restore seabirds to an area once the threats have been removed. Such actions include: the use of decoys, playing of seabird call, translocation, habitat improvement including addition of nest-boxes and restoration of native plants (Jones and Kress 2012, Kappes and Jones 2014). Any actions that restore seabirds to nesting habitats that are not currently being utilized will have compounded positive effects for the ecosystem. Not only will re-introduced seabirds deposit important



nutrients, but the restoration actions themselves seabirds have cascading effects throughout the ecosystem (Benayas et al. 2009b, Eijzenga et al. 2011, Pender et al. 2013).

Table 2.1. Seabirds breeding on the main Hawaiian Islands (MHI) in recent or historical times.

Family	Common Name	Scientific name	Conservation status	Estimated current population (MHI) <sup>1</sup>	Estimated nesting density (m <sup>2</sup> )	Breeding islands
diomedeidae	Laysan albatross	<i>Diomedea immutabilis</i>	NT	650	0.011–0.79 <sup>2,4</sup>	Ni‘ihau, Kaua‘i, and O‘ahu
	Black-footed albatross	<i>Phoebastria nigripes</i>	VU	30	0.05–0.25 <sup>3,4</sup>	Lehua, Ni‘ihau, NWHI
procellariidae	Hawaiian petrel	<i>Pterodroma sandwichensis</i>	VU	2,760	0.03–0.25 <sup>5</sup>	Kaua‘i, Maui, Lanai, Hawai‘i
	Bonin petrel	<i>Pterodroma hypoleuca</i>	LC	occasional	0.25–0.50 <sup>6</sup>	NWHI
	Bulwer’s petrel	<i>Bulweria bulwerii</i>	LC	1,100	0.02–0.25 <sup>3</sup>	NWHI, Islets of Lehua, O‘ahu, and Kaua‘i
	Wedge-tailed shearwater	<i>Puffinus pacificus chlororhynchus</i>	LC	67,350	0.51–1.0 <sup>7</sup>	all main islands
	Christmas shearwater	<i>Puffinus nativitatis</i>	LC	occasional	0.25–1.0 <sup>4,8</sup>	NWHI & offshore islets of main Hawaiian Islands
	Newell's shearwater	<i>Puffinus newelli</i>	EN	10,305	0.01–0.01 <sup>7</sup>	Kaua‘i, Hawai‘i, Maui

hydrobatidae	Band-rumped storm petrel	<i>Oceanodroma castro</i>	LC	240	0.69–1.0 <sup>9</sup>	Kaua‘i, Maui, Hawai‘i , Lehua
	Tristram's storm petrel	<i>Oceanodroma tristrami</i>	NT	NA	0.025–0.11 <sup>5</sup>	NWHI
IUCN conservation status: EN—endangered, VU—vulnerable, NT—near threatened, LC—least concern						
1—(Pyle and Pyle 2009)			6—(Grant et al. 1981)			
2—(Gallo-Reynoso and Figuero-Carranza 1996)			7—(Griesemer and Holmes 2011)			
3— <a href="http://nzbirdsonline.org.nz">http://nzbirdsonline.org.nz</a>			8—(Pierce et al. 2007)			
4—pers comm. Lindsay Young, Pacific Rim Conservation, Honolulu, HI			9—(Monteiro et al. 1996)			
5—(McClelland et al. 2008)						

Table 2.2. Body mass and nutrient deposition for each seabird species found in HI. Body mass averaged from values given on <http://nzbirdsonline.org.nz>.

	Weight kg	Intake(g)= Mass(g) <sup>0.72</sup>	Guano (g) produced bird <sup>-1</sup> day <sup>-1</sup>	N (g) deposited bird <sup>-1</sup> day <sup>-1</sup>
Laysan albatross	2.99	318.0	30.6	8.56
Black-footed albatross	3.25	337.7	32.5	9.09
Hawaiian petrel	0.434	79.2	7.62	2.13
Bonin petrel	0.182	42.4	4.08	1.14
Bulwer petrel	0.094	26.3	2.53	0.71
Wedge-tailed shearwater	0.435	79.4	7.63	2.14
Christmas shearwater	0.35	67.9	6.53	1.83
Newell's shearwater	0.384	72.6	6.98	1.95
Band-rumped storm petrel	0.047	16.0	1.54	0.43
Tristram's storm petrel	0.1	27.5	2.65	0.74

Table 2.3. Area (ha<sup>2</sup>) of potential historic nesting area for each island as well as estimates (kg) of potential high and low N deposition from all seabird species for each island. Lava + cliff and coast + lava+ cliff were represented by less than 0.5 km<sup>2</sup> on any island so they are net represented in this table. All categories are mutually exclusive.

Island	Lava	Cliff	Coast	Coast + Lava	Coast + Cliff	Total	Low estimate of N deposition year <sup>-1</sup>	High estimate of N deposition year <sup>-1</sup>
Hawai'i	120,800	3,000	21,200	10,100	400	155,500	83,360,000	418,000,000
Maui	1,700	7,000	19,100	700	100	28,500	64,430,000	213,400,000
Kaho'olawe	0	0	4,800	0	100	4,900	14,570,000	48,300,000
Moloka'i	0	2,800	13,800	0	800	17,400	44,910,000	144,500,000
Lāna'i	0	400	7,500	0	100	8,000	23,060,000	76,150,000
O'ahu	0	3,300	32,600	0	300	36,200	101,500,000	333,700,000
Kaua'i	0	7,100	18,200	0	900	26,100	62,040,000	196,600,000
Ni'ihau	0	0	7,000	0	100	7,100	21,200,000	70,400,000
Total	123,000	23,600	124,000	10,800	2,800	284,000	415,000,000	1,501,000,000

Table 2.4 Estimate for N deposition (kg) per ha of habitat categories.

Habitat Category	Low estimate of N deposition year <sup>-1</sup> ha <sup>-1</sup>	High estimate of N deposition year <sup>-1</sup> ha <sup>-1</sup>
Coastal	3,010	10,040
Cliff	880	1,810
Lava	370	2,570
Cliff + Lava	1,270	2,570
Cliff + Coast	1,090	1,110
Coast + lava	1,690	6,300



Figure 2.1. Newell's Shearwater chick in a burrow. (Photo by J. Rowe)



Figure 2.2. Wedge-tailed Shearwater nesting in two types of burrows.

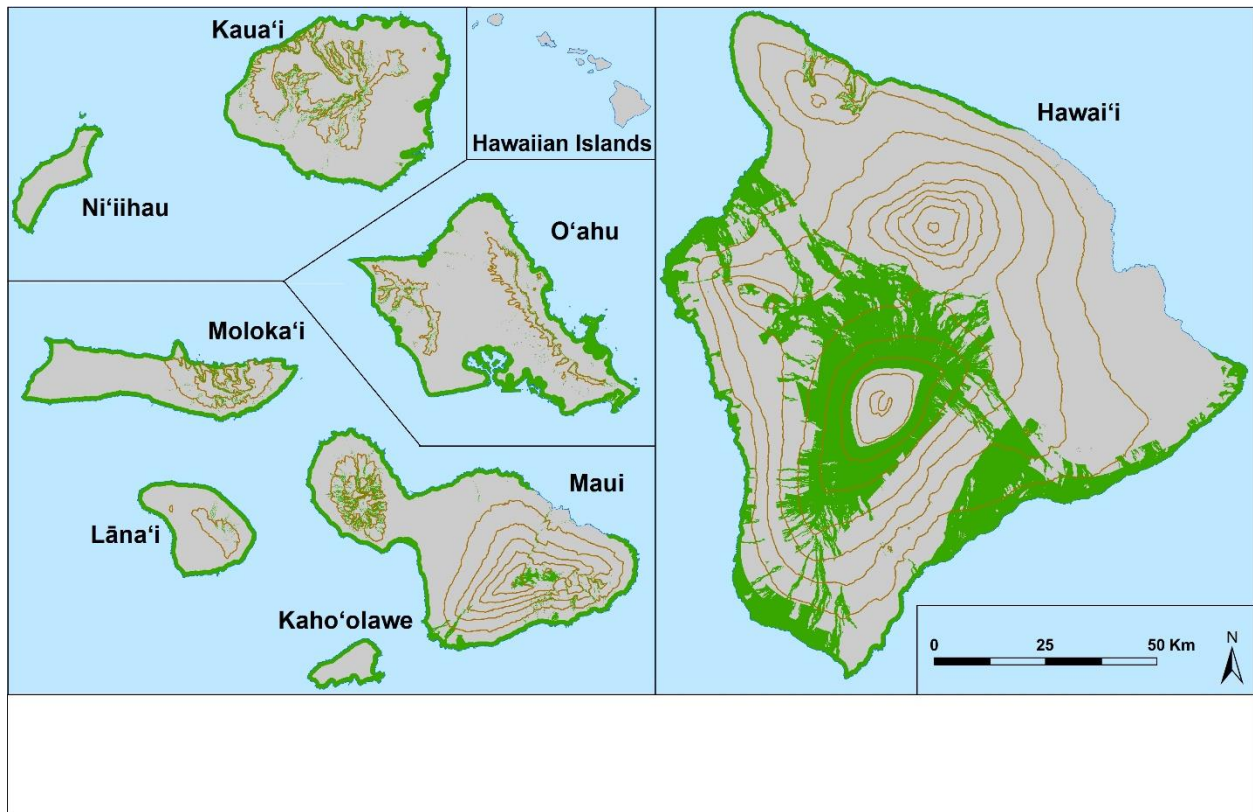


Figure 2.3. Potential historic nesting habitat across Hawaiian Islands. Green represents seabird nesting habitat. Map produced by Dr. J. Price, University of Hawaii at Hilo.



# CHAPTER 3. IMPACTS OF ENDANGERED SEABIRDS ON NUTRIENT CYCLING IN MONTANE FOREST ECOSYSTEMS OF HAWAI‘I

## Abstract

Allochthonous nutrient flow from marine sources via seabirds to the terrestrial habitats where they nest can impact resident organisms and neighboring ecosystems. Seabird populations are decreasing both in Hawai‘i and globally, yet little is known about what is being lost from the ecosystems where they traditionally nested in large numbers. Given the marked decline in seabirds, I hypothesized that the current sparsely populated seabird colonies in wet montane ecosystems of Hawai‘i contribute minimally to nutrient availability but that this small contribution should still be reflected in vegetative uptake of soil N and in plant community composition. Soil nutrient availability was assessed using ion-exchange resin probes. Plant and soil uptake of marine-derived N was determined using  $\delta^{15}\text{N}$  values in soil and foliage of the two dominant species using a two-end member N isotope mass balance mixing model. To determine if the added nutrients impacted the plant community, I also compared canopy cover (total and by dominant species), and species richness between treatments. Soil in seabird areas had more available ammonium, while nitrate and total inorganic N did not differ between sites. The dominant canopy tree, *Metrosideros polymorpha*, derived 28% of foliar N from marine sources, while this value was 15% for the dominant understory plant, *Dicranopteris linearis*. Plant species composition was not influenced by the presence or absence of seabirds. Because N plays a large role in net primary productivity, the use of marine-derived N by native plants under even limited seabird populations is likely important to the functioning of these ecosystems.

**Key words:** allochthonous nutrients, *Dicranopteris linearis*, *Metrosideros polymorpha*,  $\delta^{15}\text{N}$ .

## Introduction

Globally, seabirds can be important drivers of nutrient cycling via allochthonous deposition of nutrients such as nitrogen (N) and phosphorus (P) that influence all trophic levels in the ecosystems where they breed and nest (Anderson and Polis 1999, Mulder and Keall 2001, Whelan et al. 2008, Towns et al. 2009a, Grant-Hoffman et al. 2010). Guano naturally contains N and P, nutrients which commonly limit ecosystem processes in forest ecosystems globally (Hutchinson 1950, Elser et al. 2007). Guano composition for White-capped Noddies (*Anous minutus*) and Wedge-tailed Shearwaters (*Puffinus pacificus*) is approximately 7.3% N and 1.5% P (Smith and Johnson 1995), but N content of guano increases to 14.9–28.6% for pelagic seabirds such as Northern Fulmar (*Fulmarus glacialis*) and Manx Shearwater (*Puffinus puffinus*) (Burger et al. 1978, Bird et al. 2008). As such, seabird defecation can increase available pools of N and P in terrestrial ecosystems by 100 and 400 times, respectively (Mulder et al. 2011). In turn, marine-derived nutrient subsidies affect a suite of processes including primary productivity (Mulder and Keall 2001), plant community composition (Anderson et al. 2008, Mizota 2009), and the population size of top predators (Rose and Polis 1998).

The role of seabird guano in the transport of nutrients from marine sources to land has been studied in many coastal ecosystems, but tropical montane ecosystems where many burrowing seabirds nest have been poorly studied (Mulder et al. 2011). Nutrient levels in highly weathered tropical ecosystems can be low, particularly for P, and with high rainfall and steep slopes N and P can be readily lost through leaching and erosion (Ehleringer et al. 1986, Posada and Schuur 2011). In these nutrient poor ecosystems, the addition of N and P rich guano may be vital to maintaining or enhancing plant communities and ecosystem process rates (Mizota 2009).

Seabirds face many challenges including habitat loss, introduction of predators, collision with man-made structures, light pollution, toxins, change in prey availability, and poisoning (Millenium Ecosystem Assessment 2005, Hebshi et al. 2008, Duffy 2010, Griesemer and Holmes 2011, Loss et al. 2012, 2015, Wiley et al. 2013). These challenges have typically led to severe population declines and in some cases extinctions, resulting in reduced nutrient inputs to the terrestrial habitats that seabirds traditionally occupied. In Hawai‘i, seabirds that nest in montane forest ecosystems have experienced severe population declines, with some seabird species extirpated from the Hawaiian Islands and others remaining in greatly reduced ranges and numbers (Olson and James 1994, Burney et al. 2001, Hearty et al. 2005). The decline of nutrient flux from marine to terrestrial ecosystems due to the reduction of seabirds on the main Hawaiian Islands may have significant effects on plant community dynamics and ecosystem processes. As such, understanding how native plants utilize nutrient subsidies is important to inform the conservation and restoration of native habitats.

Two seabird species that have experienced drastic population declines in the montane regions of Hawai‘i historically, as well as in the last 25 years, are the Newell’s Shearwater (*Puffinus newelli*) and Hawaiian Petrel (*Pterodroma sandwichensis*), which are federally listed as threatened and endangered, respectively (James 1990, Burney et al. 2001, Griesemer and Holmes 2011). Formerly numerous and widespread, these two species are currently limited to remote colonies in hard to access locations due to loss of habitat and an increase in introduced predators. I sought to determine whether Newell’s shearwaters and Hawaiian Petrels in low numbers still influence soil nutrient availability and plant nutrient uptake. Specifically, I sought to answer three primary research questions. First, do sparse numbers of seabirds increase the availability of macronutrients and micronutrients in wet montane forest soils? Second, do the dominant plants

in wet montane ecosystems utilize marine-derived N, and if so to what extent? Third, does avian nutrient subsidy influence plant species composition? I hypothesized that: 1) soil micronutrient and macronutrient availability would be higher around the seabird colonies than in areas without seabirds, but only minimally given the greatly reduced seabird populations (Wainright et al. 1998, Liu et al. 2006); 2)  $\delta^{15}\text{N}$  values would be higher in soil and foliage at seabird nesting sites, reflecting a marine-derived nutrient subsidy (Caut et al. 2012, Kazama et al. 2013), and; 3) the plant community composition in seabird plots would be biased towards nitrophilic plants adapted to high nutrient levels (Vitousek and Farrington 1997, Martinelli et al. 1999, Bond et al. 2010).

## **Materials and Methods**

### *Study Site*

Though greatly reduced from historic levels, the Island of Kaua‘i is home to the densest populations of montane nesting seabirds in the Hawaiian archipelago. Study sites were located in the montane forests of Upper Limahuli Preserve and Hono O Nā Pali, Kaua‘i. I considered two treatment types in each of these areas: active seabird colonies and non-seabird areas (areas without current seabird colonies and with no evidence of recent nesting) (Fig. 2.1). Notably, it is likely that seabirds historically nested in most, if not all, montane areas in the past, but the control sites contained no burrows (new or old), bird sign (e.g., feathers or guano), or records of bird activity since 2006 when the Kaua‘i Endangered Seabird Restoration Project began working in the area. Furthermore, the density of seabirds in the most heavily used areas is only 0.04 burrows  $\text{m}^{-2}$ , which is low for colonial nesting seabirds such as shearwaters and petrels which are known to nest up to 0.76 burrows  $\text{m}^{-2}$  for Grey-faced Petrel (*Pterodroma macroptera gouldi*;

Whitehead et al. 2014) and 0.08 burrows m<sup>-2</sup> for Cook's Petrel (*Pterodroma cookie*; Rayner et al. 2007).

I established 24 plots on ridge tops: nine seabird and four non-seabird plots in Upper Limahuli Preserve and eight seabird and three non-seabird plots in Hono O Nā Pali (Figure 3.1). On the geologically older Hawaiian island of Kaua'i, ecosystem processes are typically limited by P availability (Crews et al. 1995) which is expected to apply to this study sites as well. Seabird and non-seabird plots were selected opportunistically in areas with and without seabirds, respectively. Steep slopes, lack of helicopter landing locations, and low seabird numbers made random or uniform plot selection unrealistic. Sample size for isotopic comparisons was based on an *a priori* power analysis (G\*Power version 3, 2012; Erdfelder et al. 1996). Effect size was set at 1.27 based on published soil and *M. polymorpha*  $\delta^{15}\text{N}$  values (Vitousek and Walker 1989); error probability ( $\alpha$ ) was set at 0.05 and power (1- $\beta$  error probability) was 0.95; and total sample size was calculated n=24. Each plot was 5 m in diameter and established in different seabird sub-colony clumps. The Upper Limahuli Preserve ranges in elevation from 750 to 980 m with plots located above 800 m. Hono O Nā Pali is located above 1,200 m and plots were situated between 1,210 and 1,287 m.

All soils in the two study areas were surveyed by reconnaissance survey. The soils in Upper Limahuli are classified as Alakai mucky peat and Waialeale mucky silty clay loam, while the soils in Hono O Nā Pali are classified as rough mountainous land (Soil Report for Island of Kaua'i, Hawai'i, 2014). Alakai mucky peat taxonomic classification is clayey, ferrihumic, dysic, isomesic Terric Haplosaprists with pH values typically less than 4.0. Waialeale mucky silty clay loam is classified as very-fine, isotic, isothermic Typic Epiaquods with pH values commonly less

than 4.4. Based on similar topography and rainfall it is likely that the rough mountainous land in Hono O Nā Pali has the same classification as the soils in Upper Limahuli.

All plots were located in wet montane forest with the majority of vegetation being native and dominated by *Metrosideros polymorpha* (ohia) in the canopy and the staghorn fern *Dicranopteris linearis* (uluhe) in the understory. No N fixing plants were present, although there is evidence of N-fixation in the litter of *D. linearis* (Russell and Vitousek 1997). Mean annual precipitation at both sites ranges between 2,500 and 3,000 mm with rain occurring throughout the year (Giambelluca et al. 2013). Mean annual temperature is 13°C, with warmest temperatures occurring in August and September (Juvik and Juvik 1998). Both study sites are remote with relatively intact forests exposed to introduced pigs (*Sus scrofa*), cats (*Felis catus*), mice (*Mus musculus*), and two rat species (*Rattus exulans* and *Rattus rattus*). In recent years, control and restoration measures have been implemented, including ungulate-proof fencing and pig removal in Upper Limahuli, and trapping for invasive animals and nonnative plant removal in both sites (Jon-Carl Watson, Limahuli Preserve Operations Manager at National Tropical Botanical Garden pers. comm).

#### *Available Soil Nutrients*

To assess the availability of inorganic soil macronutrients and micronutrients, plant root simulator (PRS) probes (Western Ag Innovations Inc., Saskatchewan, Canada) were deployed in the top 5–10 cm of mineral soil. The PRS probes consist of separate anion and cation exchange membranes that assess nutrient supply rates by continuously absorbing charged ions over the period that they are in the soil. Nutrients indexed represent the bioavailable, labile, inorganic pools in the forms of  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ ,  $\text{H}_2\text{PO}_4^{3-}$ ,  $\text{SO}_4^{2-}$ ,  $\text{K}^+$ ,  $\text{Mg}^{2+}$  and  $\text{Ca}^{2+}$  (Johnson et al. 2005,

Meason and Idol 2008, Beyene and Katzensteiner 2011). To account for soil heterogeneity, eight pairs of PRS probes were deployed per plot (192 total) during peak to late seabird breeding season (September 8–October 9, 2013). The probes were retrieved after four weeks, when they were presumed to have reached a dynamic equilibrium (Meason and Idol 2008, Beyene and Katzensteiner 2011). Probes were rinsed with deionized water to remove roots and soil, and shipped to Western Ag Innovations Inc. for extraction and analysis. Nutrients were extracted by shaking the probe in 35 mL of 0.5 mol L<sup>-1</sup> HCl for 1 hour to remove > 95% of sorbed ions from the membrane. Concentrations of NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, and PO<sub>4</sub> were then analyzed using colorimetric analysis with a Technicon autoanalyser, while K<sup>+</sup>, Ca<sup>2+</sup>, and Mg<sup>2+</sup> were determined using an inductively coupled plasma spectrometer (PerkinElmer Optima 3000-DV ICP, PerkinElmer, Norwalk, CT)(Johnson et al. 2005, Meason and Idol 2008).

### *Isotopic analysis*

N isotopic ratios were determined for the top 10 cm of mineral soil, sunlit foliage of *M. polymorpha* and *D. linearis* from seabird and non-seabird plots at both sites as well as seabird guano. Samples were composited (5 soil samples, and 5 samples each of *M. polymorpha* and *D. linearis* foliage) in each plot. Soil samples were collected using a 1.27 cm diameter soil corer and sunlit, live leaves were collected from the newest fully mature cohort. Hawaiian Petrel and Newell's Shearwater guano samples were opportunistically collected from field sites during the 2014 breeding season. Twelve relatively fresh guano samples were placed in Ziploc bags and kept in a cooler on ice until they could be frozen. Organic materials were hand picked out of guano samples prior to analysis. Freshness could not be determined, but the high rainfall at these sites should preclude guano from remaining on the ground for more than two days of rain. The

mean carbon: N ratio for the sampled seabird guano was  $1.09 \pm 0.21$  ( $n = 8$ ), and  $\delta^{15}\text{N} = 8.23\text{‰} \pm 1.68\text{‰}$  ( $n = 8$ ).

Soil and foliar samples were dried at  $70^{\circ}\text{C}$ , sieved through a 2 mm mesh, homogenized, and powdered in a ball mill (Carter and Gregorich 2006). Guano samples were freeze dried and ground using a mortar and pestle. The isotopic composition of all samples was analyzed at the University of Hawai'i at Manoa Biogeochemical Stable Isotope Facility using a continuous flow mass spectrometer (ThermoFinnigan Deltaplus XP) coupled with an elemental analyzer (Costech ECS 4010) via a ConFlo IV interface. N isotopic compositions are expressed as  $\delta^{15}\text{N}$  values in ‰ relative to Air:

$$\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1000$$

where  $R_{\text{sample}}$  is the isotopic ratio ( $^{15}\text{N}/^{14}\text{N}$ ) of the sample and  $R_{\text{standard}}$  is the  $^{15}\text{N}/^{14}\text{N}$  of Air.

Accuracy and precision of  $\delta^{15}\text{N}$  values were  $< 0.2\text{‰}$ , as determined from reference materials analyzed every 10 samples (glycine and a tuna muscle homogenate with  $\delta^{15}\text{N}$  values of  $11.25 \pm 0.04\text{‰}$  and  $12.97 \pm 0.06\text{‰}$  respectively, which were determined by extensive characterization using National Institute of Standards and Technology certified reference materials and their  $\delta^{15}\text{N}$  values were verified independently in other laboratories). Percent N was determined for soil and foliage samples from the results of isotopic analysis.

A two-component N isotope mass balance mixing model was used to determine the proportion of marine-derived nutrients in the top 10 cm of soil and the foliage of the two dominant plants in the plots (Phillips and Gregg 2001, West et al. 2006). As such, I used the mixing model equation from (Dawson et al. 2002):

$$\delta T = f_A \delta A + (1-f_A) \delta B$$

$$1 = f_A + f_B$$



where  $\delta T$  is the total sampled isotopic value,  $\delta A$  and  $\delta B$  are the two source values and  $f_A$  is the portion of the total value that is provided by source A (Dawson et al. 2002). The non-seabird plot data were used to establish terrestrial  $\delta^{15}N$  end member and the  $\delta^{15}N$  value of seabird guano was used as the marine end member. Solutions from the mixing model provide the percent of total N in soil and foliage of *M. polymorpha* and *D. linearis* in the seabird plots that was marine-derived (Dawson et al. 2002, Fry 2006, Boecklen et al. 2011, Phillips 2012). Uncertainty in the marine-derived fraction of total N was determined by propagation of error using the analytical solution of the partial differentiation of general Taylor series approximation determined using the two-component stable isotope mixing model (Gelwicks and Hayes 1990, Phillips and Gregg 2001).

#### *Vegetation community assessment*

Data were collected in the same 5 m plots discussed above in Upper Limahuli and Hono O Nā Pali in collaboration with Kaua‘i Endangered Seabird Restoration Project. The following variables were quantified: % cover for each plant species taller than 2 m, % cover for each species shorter than 2 m, average vegetation height, and canopy cover. Species richness was measured by number of species per plot. To measure proportional diversity I used the Shannon index ( $H'$ ):  $H' = -\sum (p_i) \ln p_i$ ; where  $(p_i)$  is the proportion of the total number of individuals in the population that are in species “i” (Stirling et al. 2001). Percent cover of each species was used in lieu of number of individuals.

#### *Statistical Analyses*

Statistical analyses were performed in SPSS 22 (SPSS Inc. 2007). Levine’s test was used to assess homogeneity of variance in soil nutrient concentration as well as the plant community

composition. Of all nutrients analyzed (%N, total inorganic N,  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ ,  $\text{SO}_4^{2-}$ ,  $\text{PO}_4^{3-}$ , and  $\text{Ca}^{+2}$ ), only  $\text{NH}_4^+$  did not pass Levine's test and these data were  $\log_{10}$  transformed for analysis. All plant community composition data passed Levine's test. One-way ANOVA, with significance set at  $\alpha = 0.05$ , was used to test for differences in available soil nutrients as well as relative differences in  $\delta^{15}\text{N}$  values in soil and *M. polymorpha* and *D. linearis* foliage between treatments. All results are presented as means  $\pm$  SE, unless otherwise noted. I used t-tests to determine differences between treatments for % N in *M. polymorpha* and *D. linearis*. For plant community composition; I analyzed canopy cover, average vegetation height, total *Metrosideros* cover, and total number of species present to look for differences between treatments also using *t*-tests.

## Results

### *Available soil nutrients*

Across all measured inorganic soil nutrients, only the concentration of  $\text{NH}_4^+$  showed higher values in the seabird plots compared to non-seabird plots ( $F_{1,21} = 4.74$ ,  $p = 0.04$ ) (Table 3.1). Total inorganic N availability did not differ between treatments, largely because the availability of  $\text{NO}_3^-$  was nearly identical between seabird and non-seabird plots. In addition,  $\text{PO}_4^{3-}$ ,  $\text{Ca}^{+2}$ , and  $\text{SO}_4^{2-}$  were slightly, but not significantly, lower in seabird plots (Table 3.1).

### *Isotopic analysis*

Foliage of *M. polymorpha* had significantly higher  $\delta^{15}\text{N}$  values in the seabird than in the non-seabird plots ( $F_{1,21} = 5.07$ ,  $p = 0.036$ ; Table 3.2). Although  $\delta^{15}\text{N}$  values in soil and *D. linearis* leaves between the two treatments were not statistically different ( $F_{1,21} = 2.78$ ,  $p = 0.11$ ;  $F_{1,21} = 2.82$ ,  $p = 0.11$ , respectively), there was a positive trend towards increasing  $\delta^{15}\text{N}$  values in the

seabird plots compared to the non-seabird plots (Table 3.2). Results from the mixing model indicated that 32% of the total soil N was derived from seabirds in the seabird plots. Foliar N of *M. polymorpha* in seabird plots was 27.9% (8% SE) from marine source, while *D. linearis* foliage contained 16.9% (0.08 SE) N from a marine source (Table 3.3). However, % N did not differ between seabird and non-seabird plots (Table 3.4) for soil ( $t_{32} = 0.81$ ,  $p = 0.43$ ), *M. polymorpha* foliage ( $t_{20} = 0.17$ ,  $p = 0.26$ ), or *D. linearis* foliage ( $t_{21} = 0.92$ ,  $p = 0.37$ ).

### *Plant Community Composition*

Seabird and non-seabird plots had similar species composition and vegetation structure. Specifically, canopy cover ( $t_{22} = -0.13$ ,  $p = 0.21$ ), average vegetation height ( $t_{22} = -0.20$ ,  $p = .84$ ), total *M. polymorpha* cover ( $t_{22} = -1.35$ ,  $p = 0.19$ ), total species recorded ( $t_{22} = 0.48$ ,  $p = 0.96$ ), and  $H'$  ( $t_{22} = 0.038$ ,  $p = 0.97$ ) were all similar between treatments.

## **Discussion**

I found support for the first hypothesis in that more inorganic N in the form of  $\text{NH}_4^+$  was found where seabirds were present. In support of the second hypothesis, 32% of soil N was of a marine source, and that marine-derived N accounted for 17–28% of foliar N in the two dominant native plants in the study system. However, I did not find evidence to support the third hypothesis that plant community composition would differ with and without allochthonous input of nutrients by seabirds.

Microbial processes can affect the N isotopic composition of plant-soil systems (Amundson 2003, Szpak 2014). N in guano is deposited primarily as uric acid ( $\text{C}_5\text{H}_4\text{O}_3\text{N}_4$ ; Bird et al., 2008) and microbes mineralize this organic N into  $\text{NH}_4^+$  and  $\text{NO}_3^-$ . Inorganic N as  $\text{NH}_4^+$

and  $\text{NO}_3^-$  is available to most plants in soil solution, making this a potentially important addition to the ecosystem. Ammonium can be lost from the system through oxidation (the first step in soil nitrification), which can lead to N loss as nitrates are leached from the soil or through ammonia volatilization. N transformations such as ammonia volatilization and denitrification can affect the  $\delta^{15}\text{N}$  values of plants and soil because there are large N isotope fractionations associated with these processes. I do not however believe that N loss in the studied systems studied was the main cause of  $^{15}\text{N}$  enrichment in seabird sites. The soil types in these areas are acidic (pH less than 4.5) and under these acidic conditions ammonia would be protonated so that the dominant form of reduced N would be non-volatile ammonium. In Hawaiian rainforests in regions with mean annual rainfall exceeding ~2,500 mm, soil microbial denitrification completely consumes nitrate in local soil environments, preventing expression of the isotope effect associated with denitrification (Houlton et al. 2006). Under these conditions  $\delta^{15}\text{N}$  values of soils converge on the  $\delta^{15}\text{N}$  values of the N input. I anticipate that these potential losses of N may make seabird subsidies more critical to the ecosystem than currently understand.

The impacts of seabirds on soil and plant characteristics vary across systems and depend at least partially on the life history of the seabirds in question. Durrett et al. (2014) found that trees and shrubs differed in their response to the addition of marine nutrients with trees increasing slowly in foliar %N and  $\delta^{15}\text{N}$  values with increasing population density while shrubs showed a strong positive response at low densities and negative responses at higher densities. In ecosystems that are N and/or P limited, the addition of guano may increase primary productivity and select for fast growing plants that can take advantage of periodic resource subsidies, or seabirds that nest in high density may make the soils toxic to plants with the excessive addition of nutrients (Wainright et al. 1998, Anderson and Polis 1999, Kolb et al. 2010). In similar studies

based on coastal seabird colonies, nutrient pulses caused changes that were observed through the food web and even back into the marine environment. These changes included increased plant productivity, increased plant predation, increased arthropod and lizard density, and increased coastal nutrient influx into the nearshore environment leading to increased plankton growth (Barrett et al. 2005, Spiller et al. 2010, McCauley et al. 2012). On Kaua‘i, Newell’s Shearwater and Hawaiian Petrel nest colonially, but in low densities in burrows. As burrow nesting birds are not observed to reach densities that cause nutrient toxicity to plants, seabirds likely played a larger supporting role historically in nutrient cycling in this ecosystem when population numbers were higher.

I estimated the quantity of nutrients potentially added to the study sites by guano input. The two sites total about 200 ha, 160 ha in Upper Limahuli and 40 ha in Hono O Nā Pali, including non-seabird areas as well as areas where the seabirds are nesting. There are no official estimates of seabird population numbers in these areas, but using Griesemer’s island wide estimates for Newell’s Shearwater as well as estimates from the field, I estimated 500 pairs ( $\pm$  250) of Newell’s Shearwater and Hawaiian Petrel combined between the two sites with proportionally more Newell’s Shearwater in Upper Limahuli and proportionally more Hawaiian Petrels in Hono O Nā Pali (Griesemer and Holmes 2011). No studies have been conducted to indicate how much Newell’s Shearwater or Hawaiian Petrel eat or excrete per day. However, the wandering albatross weighs approximately 10 kg and was found to consume two kilograms of food per day (Salamolard and Weimerskirch 1993). The average weight for Newell’s Shearwater and Hawaiian Petrel is 0.4 kg (Ainley et al. 1997, Judge et al. 2014). Therefore, since small organisms require more food per unit body mass than larger organisms, I used the allometric relationship:

$$\text{Intake(g)} \sim \text{Mass(g)}^{0.72} \text{ (Schneider 2002)}$$

to estimate food intake, assuming birds are in homeostasis. Doing this I estimated that seabirds in our study sites consume 0.2 kg of marine-based food per day. Based on the seabird intake and calculations of guano production in dovekeys (Gabrielsen et al. 1991), I estimated that 500 seabirds could produce 98.5 kg of guano day<sup>-1</sup>, or 73.9 kg ha<sup>-1</sup> y<sup>-1</sup>. Not all of the guano would end up in the montane ecosystem as one bird of a pair would likely be out to sea, so half of this estimate is 37 kg guano ha<sup>-1</sup> y<sup>-1</sup>. Estimating the N content of the guano at 22% yields 16 kg N ha<sup>-1</sup> y<sup>-1</sup> (Bird et al. 2008). For comparison, total N deposition from precipitation was measured as 1 kg N ha<sup>-1</sup> y<sup>-1</sup> at a site on Hawai'i Island (Vitousek 2004). *Acacia koa*, a dominant native symbiotic N fixing tree, was not present in our sites but estimates of N<sub>2</sub>-fixation in dense regenerating *A. koa* stands range from 23 kg N ha<sup>-1</sup> y<sup>-1</sup> in 5-year-old stands to 1.5 kg N ha<sup>-1</sup> y<sup>-1</sup> in 20 year old stands (Pearson and Vitousek 2002).

### *Isotopic analysis*

Seabirds have been shown to increase N levels in soil and surrounding organisms via marine-derived N (Wainright et al. 1998, Wait et al. 2005, Mizota 2009). However, it was previously unknown if this is also the case in wet tropical montane regions characterized by high rainfall, warm temperatures, and low current population densities of seabirds (Martinelli et al. 1999, Garcia et al. 2002). While marine N was clearly higher in *M. polymorpha*, the effect of seabird added N may be masked in *D. linearis* by N fixation that may occur in the litter (Russell and Vitousek 1997). It should also be kept in mind that although the non-seabird sites had no current evidence for nesting, they were likely colonized in the past and may have a legacy of high  $\delta^{15}\text{N}$  values in soil. Thus, using these non-seabird sites likely resulted in an overestimation of

terrestrial  $\delta^{15}\text{N}$  end member values in the isotope mass balance mixing model, and thus systematically underestimated the proportion of marine-derived N available in the soil and incorporated into the foliage of both studied species.

Researchers have measured  $\delta^{15}\text{N}$  of *M. polymorpha* foliage in non-seabird areas in Hawai'i across multiple islands and found mean  $\delta^{15}\text{N}$  values of -3.3 ( $\pm 2.3\%$  SD) and -2.8 ( $\pm 2.6\%$  SD) (Vitousek et al. 1989, Martinelli et al. 1999). A comparison of their values with this study are complicated by difference in substrate age between sampling sites in these prior studies and ours on Kaua'i. Martinelli et al. (1999) also measured a  $\delta^{15}\text{N}$  value of -0.5‰ from a single *M. polymorpha* on Kaua'i from a non-seabird area. It is unknown if the  $\delta^{15}\text{N}$  value of -0.5‰ is an outlier or representative of *M. polymorpha* on Kaua'i. However, the archipelago averages of -3.3‰ and -2.8‰ in non-seabird areas are slightly lower than the non-seabird values that I measured for *M. polymorpha* (-2.3‰), and this also indicates a potential underestimate of the importance of current marine-derived N as presented here.

Results of the isotopic mixing models indicate that dominant plants in this ecosystem utilize at least some N derived from a marine source, and soil and foliage of both plant species showed marine influence. Although standard error was high, the amount of marine sourced N was higher across all sampled substrates in seabird plots, and  $\delta^{15}\text{N}$  values were significantly higher in *M. polymorpha* foliage in seabird plots compared to control plots.

#### *Plant community composition*

None of the plant species composition measures indicated differences between seabird and non-seabird plots. This is likely due to not only the limited amount of nitrogen being added to the seabird sites, but also the species depauperate nature of the islands and isolation of the study

sites. There are a limited number of native species on the islands to populate these areas and the isolated nature of the study sites means less influence of the nonnative and invasive plant species that occur in high densities in more disturbed areas in Hawai‘i. Invasive plant species were actively managed in Upper Limahuli and pulled opportunistically in Hono O Nā Pali, though the density of invasive plants is low in both sites due to the remote locations. Another reason for the lack of differences in some of the measured variables is that other drivers besides the addition of nutrients by seabirds may be more influential, particularly in low density seabird sites such as ours. Other researchers found that on high and medium density seabird islands, seabirds drove ecosystem properties such as  $\delta^{15}\text{N}$  values (soil and leaf), soil and leaf N,  $\text{NH}_4^+$ , and  $\text{NO}_3$ . However, in low density colonies other ecosystem processes drove these ecosystem properties more than the seabirds (Durrett et al. 2014).

## **Conclusion**

Despite being at historically low population densities, seabirds contribute to the ecosystems where they still nest in montane Hawai‘i via marine-derived nutrient deposition. These study sites in Kaua‘i contain some of the last relatively intact tropical montane ecosystem with native seabirds, yet very little research has occurred there. Studies in the arctic and in coastal systems are abundant (Polis and Hurd 1996, Mulder et al. 2011, Gagnon et al. 2013), and generally show that seabirds increase nutrient availability and biodiversity (Keatley et al. 2009, Zmudczyńska et al. 2012), and that they fertilize or even create toxic conditions in coastal ecosystems depending on seabird density (Kolb et al. 2010, VanderWerf et al. 2014). However, comprehensive studies about how seabirds and their nutrient subsidies impact tropical montane ecosystems are notably lacking (Hawke and Holdaway 2009).



The control plots in this study may have a historical legacy of seabirds and thus may still contain nutrients from seabirds. Therefore, our estimate of allochthonous nutrient input by seabirds is likely conservative. The influx of N and P may be more important to the resiliency of these ecosystems, especially in the face of climate change and other stressors, than is currently understood (Perry, Goerge et al. 2010, Doughty et al. 2015). Historically seabirds in the Hawaiian Islands may have played a leading role in controlling soil fertility in areas where they nested. The montane forest seabirds in the Hawaiian Islands have been greatly reduced both in number and in range, yet even in vastly reduced numbers these birds continue to impact soil and vegetation nutrient content. The decrease in nutrient flow and its impacts on the ecosystem are vital for restoration project managers to understand as they attempt to rebuild the ecosystem and restore endemic plants and wildlife.

Table 3.1. Mean and Standard error (SE) of inorganic soil nutrient availability for seabird and non-seabird plots ( $\mu\text{g}/10\text{ cm-2}/4\text{ weeks}$ ). Results in bold indicate significant differences between seabird and non-seabird plots at  $p < 0.05$ . Total N refers to total inorganic N.

		mean	SE	F	df	p
Total N	Seabird	59.4	14.7	0.595	1/21	0.449
	NonSeabird	36.5	17.6			
$\text{NO}_3^-$	Seabird	23.5	11.2	0	1/21	0.988
	NonSeabird	23	15.8			
$\text{NH}_4^+$	<b>Seabird</b>	<b>36</b>	<b>0.1</b>	<b>4.74</b>	<b>1/21</b>	<b>0.041</b>
	<b>NonSeabird</b>	<b>13.8</b>	<b>0.1</b>			
$\text{SO}_4^{2-}$	Seabird	47.15	11.4	0.046	1/21	0.833
	NonSeabird	52.4	22.6			
$\text{PO}_4^{3-}$	Seabird	5.3	1.6	0.272	1/21	0.607
	NonSeabird	7.2	3.6			
$\text{Ca}^{2+}$	Seabird	155.1	26.7	0.019	1/21	0.891
	Non-Seabird	146.8	138.5			

Table 3.2. Mean and standard error (SE) of  $\delta^{15}\text{N}$  values of soil and two dominant plant species in seabird and non-seabird plots on Kaua'i. Results in bold indicate significant differences between seabird and non-seabird plots at  $p < 0.05$ .

		mean	SE	F	df	<i>p</i>
Soil	Seabird	1.23	0.31	2.82	1	0.108
	Non-seabird	-0.183	0.62			
<i>Metrosideros</i>	<b>Seabird</b>	<b>0.65</b>	<b>0.76</b>	<b>5.07</b>	<b>1</b>	<b>0.036</b>
	<b>Non-seabird</b>	<b>-2.26</b>	<b>0.46</b>			
<i>Dicranopteris</i>	Seabird	6.06	0.46	2.77	1	0.109
	Non-seabird	5.04	0.56			

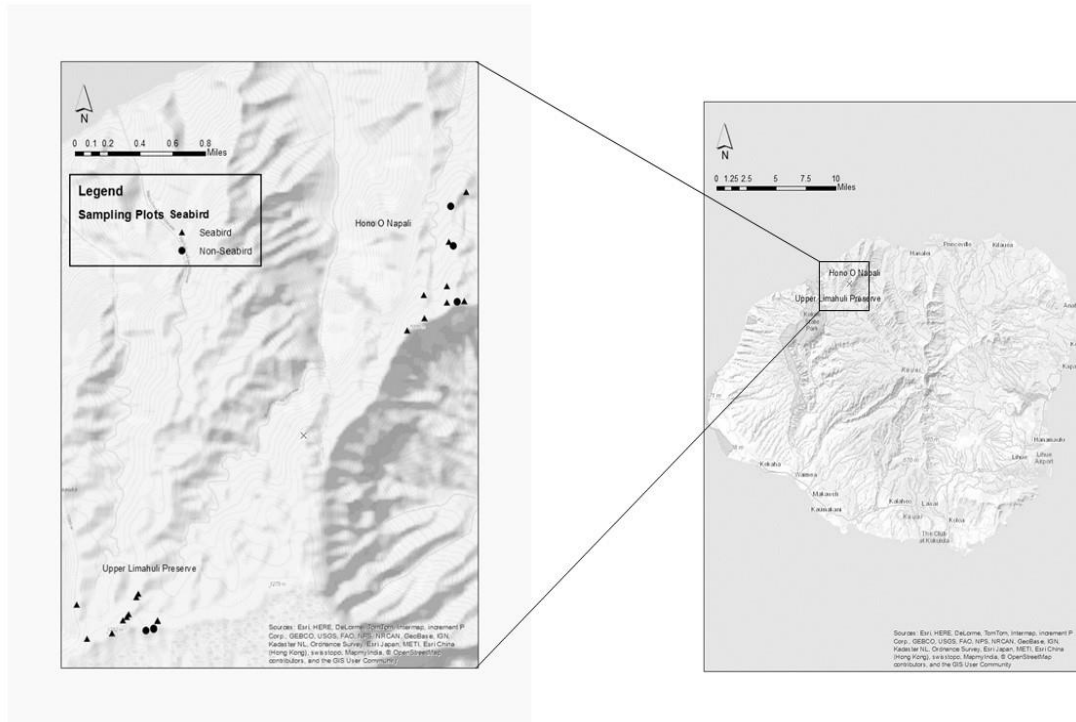
Table 3.3. Mean proportions and propagated error for a two source, one isotope ( $\delta^{15}\text{N}$ ) model for soil and two dominant plant species in seabird and non-seabird plots. Values reported are means and standard error, calculated as per Phillips and Gregg (2001). Input values for the seabird substrates and source 1 and source 2 are also listed.

	Seabird			Source 1 – plots with no seabird nests			Source 2- guano
	Soil	<i>M. polymorpha</i> foliage	<i>D. linearis</i> foliage	Soil	<i>M. polymorpha</i> foliage	<i>D. linearis</i> foliage	
$\delta^{15}\text{N}$ (‰) (SE)	6.1 (0.30)	0.7 (0.76)	1.2 (0.46)	5.0 (0.63)	-2.3 (0.46)	-0.2 (0.56)	8.2 (1.7)
Sample Size	19	16	17	11	6	6	8
Proportion of N from marine source (SE)	32% (0.18)	27.9% (0.08)	16.9% (0.078)				
95% Confidence Limits	0–69%	11–45%	0–34%				

Table 3.4. Mean %N in soil, *M. polymorpha*, and *D. linearis*.

		mean $\pm$ SD	t	<i>p</i>
soil	seabird	0.54 (0.21)	$t_{32} = 0.81$	0.43
	non-seabird	0.48 (0.25)		
<i>D. linearis</i>	seabird	1.2 (0.19)	$t_{20} = 0.17$	0.26
	non-seabird	1.28 (0.22)		
<i>M. polymorpha</i>	seabird	0.66 (0.09)	$t_{21} = 0.92$	0.37
	non-seabird	0.61 (0.10)		

Figure 3.1. Location of plots in Upper Limahuli Preserve (ULP) and Hono O Na Pali (Pihea), Kaua‘i, HI. Seabird plots are represented with a triangle and non-seabird plots are represented with a circle.



## **CHAPTER 4. THE COSTS AND ECOSYSTEM SERVICE BENEFITS OF SEABIRD RESTORATION IN HAWAI'I**

### **Abstract**

Given the importance of seabird restoration efforts, my goal in this chapter was to ascertain if restoration actions taken had higher ecosystem services benefits than others and if that correlated with cost. I hypothesized that restoration projects that utilized predator proof fencing would show the most ecosystem services benefit and that fencing, whether it was ungulate-proof or predator proof, would have higher ecosystem services values. The method used to compare the costs was to calculate the Net Present Value for each project and correlate cost with the size of the projects. Eleven of 15 state, private, and non-government organizations and agencies that had projects focused on seabird restoration currently or between 2005–2015 participated in the cost/benefit survey. Estimated costs ranged from \$2,735 to \$341,884 ha<sup>-1</sup>. I developed a rubric to qualitatively assess the ecosystem services benefits for the restoration projects. There was no significant difference in ecosystem services benefits based on whether there was no fence, an ungulate fence, or predator-proof fencing. There were also no cost differences per hectare related to size of restoration project. While there were no differences in ecosystem improvement between fencing types, it is worth noting that all restoration activities were associated with an increase in at least two of four measured ecosystem services. The location of the projects and the threats that had to be addressed, both made large impacts on costs and realized benefits for each project.

## **Introduction**

Seabird species population status has declined over the last several decades due to threats they face both on land and at sea (Rands et al. 2010, Croxall et al. 2012, Welch et al. 2012). On land where seabirds nest, ecosystems are deteriorating and other native species are declining with limited funds for their restoration (Dobson et al. 2006, Jones and Kress 2012). Ecological restoration efforts have increased over the last decade to mitigate the threats that seabirds face and to restore nesting habitats (Jones and Kress 2012, Ismar et al. 2014, Kappes and Jones 2014). These efforts work to reestablish ecosystem services and improve ecosystem health (Figure 4.1; Benayas et al. 2009). However, due to the ongoing aspect of most seabird restoration projects, long-term funding is one most important factors to a successful restoration project (Jones and Kress 2012). Seabirds often nest in remote locations with difficult terrain that makes island restoration expensive (Holmes et al. 2016, Mazziotta et al. 2016). To successfully restore seabirds, managers need to understand the ecological causes of the declines and determine the management or restoration actions needed. Since budget constraints usually limit the activities that can be undertaken, understanding the direct and indirect impacts of management actions can maximize benefit for the available funding (Bellingham et al. 2010, Jones and Kress 2012).

Globally, invasive species are the greatest threat to island ecosystems and seabirds (Mooney and Cleland 2001, Jones et al. 2008, Plentovich et al. 2009, Glen et al. 2013) while collision and light pollution are problems in many other areas as well. Seabirds in Hawai‘i face the same threats. The top three causes of seabird mortality in the Hawaiian Islands are: predation, collision with man-made structures and fallout from light during fledging season (Ainley et al. 2001, Griesemer and Holmes 2011).



Studies have shown that restoration projects considering the economic costs as well benefits are able design more cost effective restoration budgets than those projects which fail to do so (Naidoo et al. 2006). Often these benefits are referred to as “ecosystem services” to reflect their benefit to society (Daily 1997). Obvious direct benefits of seabird restoration are the increase in seabirds (valuable in and of itself or for viewing) and by extension biodiversity (Bancroft et al. 2005). Additional ecosystem services that result from seabird restoration include nutrient deposition from marine sources to terrestrial ecosystems and biodiversity. Seabirds bring in large quantities of nitrogen (N) and phosphorus (P) from the ocean to their nesting colonies on land (Polis and Hurd 1996, Wainright et al. 1998, Sanchez-Pinero and Polis 2000, Ellis 2005, Spiller et al. 2010).

On the main islands of Hawai‘i, seabird species nest almost anywhere that they can build a nest and avoid predation. They nest on pahoehoe lava fields, in wet montain forest, along the coast in low vegetation, and in cliffs. Every island in this study is home to plants and animals found no where else in the world, and yet, the priciples of ecological restoration and economic analysis can be applied here as well as other restoration sites globally (Figure 4.2). My goal with this research was to evaluate/quantify the costs and benefits associated with seabird restoration within an island context. Because predator-proof fences keep out all invasive mammals, I hypothesized that the most expensive restoration action, predator-proof fencing, would be associated with the highest ecosystem service benefits, I also hypothesized that any fencing would be associated with higher ecosystem service benefits than the non-fenced areas since ungulates and rats are detrimental to native flora (Scofield et al. 2011, Young et al. 2012, 2013, Ismar et al. 2014). Better management decisions can be made by incorporating analysis of net change in ecosystem services.

## Methods

### *Study Area and Survey Subjects*

To address my goal conducted a cost and ecosystem service assessment of seabird restoration projects in Hawai‘i. I located and identified restoration projects by conducting an internet search using the keywords of “Hawai‘i” + “seabird” + “restoration.” I then asked managers from these projects to identify any other seabird restoration projects in Hawai‘i. During this search, I identified 15 state, private, and non-government organizations and agencies that had projects focused on seabird restoration currently or between 2005–2015. Potential participants were contact by e-mail to determine their interest in participating in this research and then by phone to further explain the research and answer questions. Bird species that managers were working to conserve or restore included: Black-footed Albatross (*Phoebastria nigripes*), Hawaiian Petrel (*Pterodroma sandwichensis*), Laysan Albatross (*Phoebastria immutabilis*), Newell’s Shearwater (*Puffinus newelli*), and Wedge-tailed Shearwater (*Puffinus pacificus*). Managers of 12 projects agreed to work with me.

Passive techniques are those that remove the threat to the target organism and then allow the population to recover on its own. Active restoration includes activities to actively bring the target organism to the site and encourage breeding. In this context active techniques would include chick translocation and social attraction measure such as decoys in the colony area and playing calls of the target bird (Jones and Kress 2012, Buxton et al. 2016). This study focused on passive restoration actions such as rodent eradication or invasive plant removal. The use of active restoration techniques were too infrequent in these projects to include in this analysis. With this study I focused on the indirect benefits that come from the restoration action itself (Table 4.1, Figure 4.1). Indirect benefits in this project include improvements in ecosystem

services such as: erosion control, conservation of biodiversity, habitat for native organisms, and seedling recruitment. For instance, removing rats (*Rattus rattus*, *Rattus exulans*) from a site not only lessens the predation on seabirds, chicks, and eggs (direct effect and primary objective), but also may increase seedling recruitment and increase biodiversity (indirect effects and secondary objectives).

### *Data Collection*

To assess the indirect impacts of restoration, I focused on the following ecosystem services: (1) erosion control, (2) conservation of biodiversity, (3) habitat creation and improvement for native organisms, and (3) seedling recruitment (Table 4.2). These were chosen based on previous work from New Zealand (Lee et al. 2005, Towns et al. 2009b) that also included performance measures that assessed indirect benefits: (i) maintaining ecosystem processes, (ii) reducing the spread and impact of invasive species, (iii) preventing declines and extinctions of native species, (iv) improving ecosystem composition, and (v) community participation in conservation. As with Towns et al. (2009) each ecosystem service category was assigned a binned, integer response from 0 for no change to 4 for the most change. Ecosystem services evaluated and categories were determined with expert input from researchers and project managers involved in this research project. Descriptions for each binned category of ecosystem service improvement were included for all ecosystem services surveyed (Table 4.2). All respondents were asked to rate the effectiveness of each restoration action since the start of the project on each of the ecosystem services. Respondents were unable to separately assess the influence of each restoration action on each ecosystem service, therefore, the impact of the entire project, which constituted bundles of restoration activities, was assessed for each service.

Information about the actual and estimated costs associated with each restoration activity, including ungulate and predator proof fencing (Figure 4.3), predator eradication, plant removal, native plantings, and monitoring came from participants' responses to interviews (Appendix 1). Fifteen project managers were identified and project managers of 11 projects participated. At least one week before the interview I sent managers the interview outline (Appendix 1) and a consent form. The phone interview addressed the types of actions that seabird managers implemented to restore seabird species in Hawai'i, the costs of these actions, the time-frame of the project's activities, and their assessment of the project's impact on specific ecosystem services (see Table 4.2 for the ecosystem services rubric). The survey was evaluated by the University of Hawai'i at Mānoa's Office of Research Compliance Committee on Human Subjects (CHS #22180).

For each restoration activity, I recorded initial costs and annual recurring costs. Since projects differed in size, I report costs as per hectare (ha) to allow for comparison. Cost of restoration actions ( $n = 36$ ) across projects ( $n = 12$ ) were calculated as initial costs/ha and annual costs/ha. Initial input costs (I) are the cost of all materials, time, and labor per hectare that were invested at the beginning of the project. Materials included items such as batteries for cameras or song meters, bait for traps, replacement memory cards, replacement traps, fuel for vehicles, and vehicle maintenance. Fencing costs included materials, labor, and transportation. Fence maintenance was considered a separate recurring cost. Recurring costs (R) were the sum of labor and routine material input per hectare per year. Incremental cost (In) includes the cost per hectare of items that must be replaced on a regular basis, but less frequently than every year. Costs were measured in USD. For project comparisons, costs were calculated as:  $\text{Cost of action} = \Sigma \text{costs} / \Sigma \text{hectares} / \text{year}$  (Kessler et al. 2013). Finally, the present value of the costs (NPV) were calculated

using an annual discount rate of 5% (Gardner et al. 2008, Birch et al. 2010) and an inflation rate of 1.5% (U.S. inflation rate 2017).

I did not assess how well the restoration actions achieved the primary goal of increasing seabird populations. Most of these projects were less than five years old; with seabirds delayed sexual maturity and difficulties with survey techniques, this was beyond the scope of this project (Simons 1985, Ambagis 2004, Buxton and Jones 2012, Judge et al. 2014).

### *Data Analysis*

Statistical analyses were performed in SPSS 22 (SPSS Inc. 2007). One-way ANOVA, with significance set at  $\alpha = 0.05$ , was used to test for differences in project costs by fence type as well differences in ecosystem service improvements between projects with different fence types and by vegetation restoration actions. All results are presented as mean  $\pm$  SD, unless otherwise noted. Linear regression was used to test for correlation between cost per hectare and size of projects. Net Present Value (NPV) was calculated in excel using:

$$NPV(i, N) = \sum_{t=0}^N \frac{R_t}{(1+i)^t}$$

$i$  = discount rate (5%)

$R_t$  = sum of costs of restoration actions — this has been adjusted for annual inflation at 1.5%

$N$  = project period

$t$  = year

## Results

Projects ranged in size from 2.4 ha to > 7,000 ha (mean =  $779 \pm 2,189$ ) and in operation age from 1 to 50 years, with most projects 1–5 years old (mean =  $8 \pm 14$ ). Initial project costs ranged from \$351/ha to \$137,104/ha in the first year, averaging \$36,778/ha ( $\pm \$60,433/\text{ha}$ ). Most projects (73%) involved fencing to keep the target animals out and had some form of habitat restoration, controlling non-native plants or planting native vegetation. All projects experienced improvements in at least two of the four ecosystem services evaluated.

Total initial costs were significantly different between projects with different fencing types ( $F = 4.98, p = 0.03$ ). Cost of both fence types collectively averaged \$212 ( $\pm \$223$ )  $\text{m}^{-1}$ . For projects that utilized fencing, initial outputs were greater for predator-proof fencing than for ungulate-proof fencing. Ungulate fencing costs averaged \$46 ( $\pm \$20$ )  $\text{m}^{-1}$  and predator proof fencing costs averaged \$344 ( $\pm \$223$ )  $\text{m}^{-1}$ . Recurring project costs were not significantly different between projects with different fencing regimes ( $F = 0.95, p = 0.42$ ). There was no difference in annual cost between projects with the three different fencing regimes ( $F = 1.41, p = 0.29$ ).

There was no significant difference in cost of initial predator/ungulate removal for projects grouped by fence type ( $F=1.49, p = 0.28$ ). The mean initial cost of predator/ungulate removal was \$470/ha ( $\pm \$741/\text{ha}$ ) with an annual cost of \$157/ha ( $\pm \$278$ ; Table 4.4). Not enough projects had information on recurring cost of predator/ungulate removal for comparison.

NPV of projects were widely variable between projects based on the size of projects and actions involved (Table 4.5). There was no significant correlation between project size and cost per hectare ( $F = 0.67, p = 0.43$ ). Though there appeared to be a trend (Table 4.6), there was no significant difference NPV per hectare between projects employing distinct types of fencing ( $F =$

0.27,  $p = 0.77$ , no fencing =  $\$6,887 \pm 5,000$ , ungulate fencing =  $\$20,029 \pm 25,138$ , predator proof fencing =  $\$184,840 \pm 138,748$ ).

All projects employed monitoring methods both for seabird response to restoration measures as well as for invasive mammal ingress. Several projects checked burrows for signs of activity, three were using or experimenting with song meters to monitor nocturnal activity (Figure 4.5). In every project in this study at least two categories of ecosystem services in the rubric saw improvement (Table 4.6). Most projects experienced improvement in all categories. Four of the twelve projects did not experience any erosion control improvement. Three of the projects experiencing no erosion control improvement did not have any erosion problems when the project was initiated. While provision of ecosystem services increased in every project, no significant differences were detected between groups of actions bundled by fencing type or use of vegetation restoration (Table 4.7). One project did not report ecosystem services benefit scores as the project was in the first year and they did not feel that they could assess changes yet.

## **Discussion**

There was no difference in the improvement of ecosystem service provision between projects using different fencing regime, predator-proof fence, ungulate proof fence, and no fence. Neither of my hypothesis were supported. There were no ecosystem service improvement differences between restoration actions. Costs for the different fencing regimes were as expected; initial costs for predator proof fencing were higher than ungulate-proof fencing, or no fencing, however, recurring costs were not significantly different between fencing regimes. Variance was high for recurring costs among the fencing regime choices. Another unexpected result in this study, larger projects were not more cost effective per hectare than small projects

The costs of restoration actions are important to consider early in the planning phases of any project. The projects in this study were on main Hawaiian Islands or islets in close vicinity to main islands. This proximity to humans necessitates that many of the restoration actions will need to be carried out in perpetuity as ingress from cats, rats, and other invasive species will always be a concern. The long time scales of ecosystem restoration projects mean replacement costs, maintenance, and monitoring all need to be factored in. Some costs like fence replacement occur on a 20–25-year interval, while rodent traps or game cameras must be replaced more frequently (8–10 years). These costs are subject to inflation over time. Moreover, the discount rate applied in the NPV calculation deflates costs as they occur farther into the future. I varied assumptions on inflation rates and discount rates (1.5% (US inflation rate 2016) and 5% discount rates (Birch et al. 2010)) to illustrate sensitivity in rate assumptions in planning restoration projects. Funding is considered one of the most critical limitations to seabird recovery because of the long-term nature of adaptive management required in seabird and island restoration (Mulder et al. 2011).

As was the case across many other seabird restoration projects on oceanic islands, a large focus of restoration efforts of the projects in this study was on rodent control and ungulate removal (Jones 2010). As expected, upfront costs, as well as fencing cost per meter were significantly higher for projects that utilized predator-proof fencing than no fencing or ungulate fencing. Respondents considered the large initial costs to be worth the expense due to the benefits for seabird survivorship. One manager reported that the predator-proof fence reduced the annual expenses associated with rat and mouse trapping while increasing the low herbaceous vegetation and non-target seabird nesting. Young et al. (2013) estimated that the installation of a predator-proof fence would hit financial “break even” point, where the cost of the fence equaled



the previous cost of predator removal, at approximately 16 years. In areas where ingress of cats, mongoose, rats or other small predators is especially egregious, control can be costly. Once predators were removed from an area, the cost of maintaining low to zero predator populations decreased. Though in this study, annual costs for predator-proof fencing projects tended to be higher there was no significant difference in annual cost between ungulate and predator proof fencing.

I had expected larger projects to cost less per hectare than smaller projects due to cost sharing. However, though larger projects tended to cost less per hectare than smaller projects, several outliers in each category caused this relationship to be nonsignificant. This further highlights the fact that each project is unique and may have different needs and demands than other similar projects.

Overall, each of the seabird restoration project's ecosystem services were enhanced by all combinations of restoration actions, which is consistent with other studies following seabird restoration actions (Towns et al. 2009b, 2016, Jones 2010, Ismar et al. 2014). I did not find a noticeable difference in ecosystem services response between the types of actions when I grouped them by fencing (no fence, ungulate, or predator-proof fence), by whether plants were restored, or by the size of the project. This may be a legacy of small sample size and not reflective of true differences, but I believe that it is more likely that the ecosystem services differences are more tied to the level and type of degradation of the project site before restoration and the ability to use the appropriate restoration actions. For instance, one project installed a predator proof fence and spent a large amount of money on design and rodent removal. This project did not have an erosion control problem at the outset, and native plants were already present in the site so they scored moderately across all ecosystem service categories. Therefore,

the cost is high and the benefit score is low, though it may turn out to be good for seabirds in the end, it is too early in the project to know. Another project on a smaller uninhabited island had low cost to eradicate rabbits and received high scores in all four ecosystem services categories. Therefore, it had a low cost but high ecosystem services benefits.

Removing invasive plants and creating a native plant-dominated ecosystem is important to the sustainability of the restoration efforts, and ultimately a decrease in cost output over time (Mulder et al. 2009). Non-native plant removal and native plant restoration were considered high priorities by projects aimed at restoring the entire ecosystem such as the National Tropical Botanical Garden, SunEdison, and the National Park Service. One project started with 77,000 stems of invasive strawberry guava, *Psidium cattleianum*, and > 5% native vegetation per 0.5 ha. Seven years after removing the *P. cattleianum*, controlling predators (rat species; cat, *Felis domesticus*; and barn owl, *Tyto alba*), and restoring native plants, the site contained 35% native vegetation and the calling rate of Hawaiian petrels increased from > 1 bird calling per night during the breeding season to 5–10 petrels calling per hour at night during the breeding season.

Since ungulates are known to increase erosion problems in many cases (Buckhouse et al. 1981, Merlin and Juvik 1992), erosion control was expected to be highest in projects where ungulate fencing was used, however actual erosion control impacts were less than expected in these projects. Upon closer inspection of the project specifics, it became clear that the reason for this discrepancy between outcome and expectation was because the ungulate proof fences were not used in the manner anticipated. Erosion problems were not present at the outset for two projects of the four ungulate fencing projects, one which was on lava rock and the other was using the fencing mainly to exclude dogs, humans, etc. Other projects with ungulate fencing experienced improvement in erosion control.

The framework introduced here is a step toward quantifying ecosystem service improvements and tracking them over time. A broader set of values and social perspectives need to be integrated into decision making on many levels to reach more holistic, restoration decision-making (Daily et al. 2009). These results are not intended to determine what restoration action to use per se, but rather to provide insight into the ecosystem-wide benefits associated with various management actions. Long-term monitoring of ecosystem services will allow managers to begin to understand how the actions taken for the benefit of seabird populations impact the ecosystems where they nest more holistically. Incorporating economic analysis, and integrating costs, benefits, and threats into seabird restoration project planning is vital to achieve the maximum biological benefit possible (Rey Benayas et al. 2009). This is particularly important given that many of these seabird restoration projects will have to continue monitoring and maintenance in perpetuity.

Table 4.1. Ecosystem services provided directly (D) by seabird and indirectly (I) by restoration actions.

<b>Functions</b>	<b>Ecosystem processes and components</b>	<b>Goods and services</b>
Soil retention (I)	Role of vegetation root matrix and soil biota in soil retention	Prevention of damage from erosion
Soil formation (D, I)	Weathering of rock, accumulation of organic matter	Maintenance of natural productive soils and productive ecosystems
Nutrient regulation (D)	Role of biota in storage and recycling of nutrients (N, P, &S)	Movement of nutrients from marine to terrestrial systems, nutrient pulses
Habitat Functions (I)	Providing habitat for wild plant and animal species	Maintaining biodiversity in plants and animals
Refugium function (I)	Suitable living space for wild plants and animals	Providing habitat to threatened and endangered plants and animals
Aesthetic information (I)	Attractive landscape features	Enjoyment of scenery
Recreation (D, I)	Variety in landscapes with potential recreational uses	Travel to natural ecosystems, for ecotourism, birdwatching, etc.
Cultural and artistic information (D, I)	Variety in natural features with cultural and artistic value	Use of nature as motive in books, film, painting, folklore, architect., advertising, etc.
Spiritual and historic information (D, I)	Variety in natural features with spiritual and historic value	Use of nature for religious or historic purposes
Science and education (D, I)	Variety in nature with scientific and educational value	Use of natural systems for scientific research, education, etc.

\*adapted from (Costanza et al. 1997, de Groot et al. 2002)

Table 4.2. Rubric for ecosystem services assessment.

Service	0	1	2	3	4
Erosion control	no change	25% less erosion	50% less erosion	75% less erosion	$\geq 75\%$
Conservation of biodiversity	no change	native species numbers stabilize	one new native species recorded or current native species increase	one new native species recorded and current native species increase	> one new native species established and current native species increasing
Habitat for native organisms	no change	current native plant species increase	current native plant species increase and new native species become established	new native plants established and current species well represented	increase in vegetation structure, over and understory
Seedling recruitment	no change	5% more seedlings	25% more seedlings	50% more seedlings	$\geq 75\%$ more seedlings

\*Ecosystem services defined in bin from 0–4

Table 4.3. Initial and annual cost of projects in USD categorized by fencing regimes (mean (SD)).

Item		N	mean cost ha <sup>-1</sup>	F value	P (0.05)
Initial cost	no fence	3	1,363 (508)	<b>4.98*</b>	<b>0.03</b>
	ungulate fence	4	1,301 (1,412)		
	predator-proof fence	4	86,407 (69,020)		
Annual Cost	no fence	3	2,117 (2,464)	1.41	0.29
	ungulate fence	4	927 (1,172)		
	predator-proof fence	5	86,407 (69,020)		
Cost/meter	no fence				
	ungulate fence	4	84 (15)	7.591	0.33
	predator-proof fence	4	432 (252)		

\*significant <0.05 level

Table 4.4. Initial, annual, and upfront cost in USD for predator removal per hectare for three fencing schemes presented as mean cost (SD). Annual costs per hectare are non-inclusive of incremental items.

	Initial costs ha <sup>-1</sup>				Annual costs/hectare			Upfront predator removal costs/hectare
	n	mean	high	low	mean	high	low	mean
All projects	12	36,778 (60,433)	137,104	351	2,053 (2,146)	7,048	126	470 (741)
Predator-proof fencing	5	86,407 (69,020)	137,104	3,108	2,916 (2,529)	7,048	151	955 (1,123)
Ungulate fencing	4	1,301 (1,412)	3,361	351	927 (1,172)	2,649	126	159 (141)
No fencing	3	1,363 (508)	1,778	797	2,117 (2,464)	4,958	547	249 (283)

Table 4.5 NPV in USD (\$) and ecosystem services benefit values for projects.

	NPV	NPV ha <sup>-1</sup>	Benefits			
			Erosion Control	Conservation of biodiversity	Habitat for native organisms	Seedling recruitment
Project 1	8,706,402	56,915	2	2	4	4
Project 2	737,257	12,564	2	2	4	4
Project 3	360,812	3,139	3	4	2	3
Project 4	501,565	4,958	2	4	3	4
Project 5	2,033,667	7,852	0	2	1	0
Project 6	1,059,840	341,884	0	3	3	0
Project 7	1,784,539	73,495	0	3	1	3
Project 8	42,527,008	5,531	4	4	4	4
Project 9*	2,341,242	2,735	na	na	na	na
Project 10	1,227,027	14,936	0	3	0	0
Project 11	810,945	250,486	2	2	2	2
Project 12	810,945	250,486	2	2	2	2

\*Project 9 was too new upon data collection to assess ecosystem service benefits.



Table 4.6 Average NPV (SD) in US dollars, averaged for each type of fencing option and related ecosystem services benefits. Ecosystem service scores ranged from 0 = no change to 4 = greatest change.

	NPV	NPV ha <sup>-1</sup>	Benefits			
			Erosion Control	Conservation of biodiversity	Habitat for native organisms	Seedling recruitment
Predator-proof fence	1,299,987 (572,073)	184,840 (138,748)	1	2	2	1
Ungulate-proof fence	13,700,420 (19,498,110)	20,029 (25,138)	2	3	3	3
No Fence	533,211 (190,208)	6,887 (5,000)	2	3	3	4

Table 4.7. Ecosystem service scores for projects utilizing specific restoration actions (mean scores (SD)). Possible scores range from 0 = no change to 4 = greatest change.

	Erosion control	Conservation of biodiversity	Habitat for native birds	Seedling recruitment
Ungulate Fence (n = 3)	2 (2)	3 (1.2)	2.7 (1)	2.7 (0.6)
Predator-proof Fence (n = 5)	1 (1)	2.3 (1.0)	1.8 (0.96)	1.3 (1.5)
Invasive plant removal (n = 7)	1.7 (1.5)	3.1 (0.9)	2.7 (1.1)	2.8 (1.5)
Native plant restoration (n = 6)	1.7 (1.5)	3 (0.9)	2.8 (1.2)	2.8 (1.6)

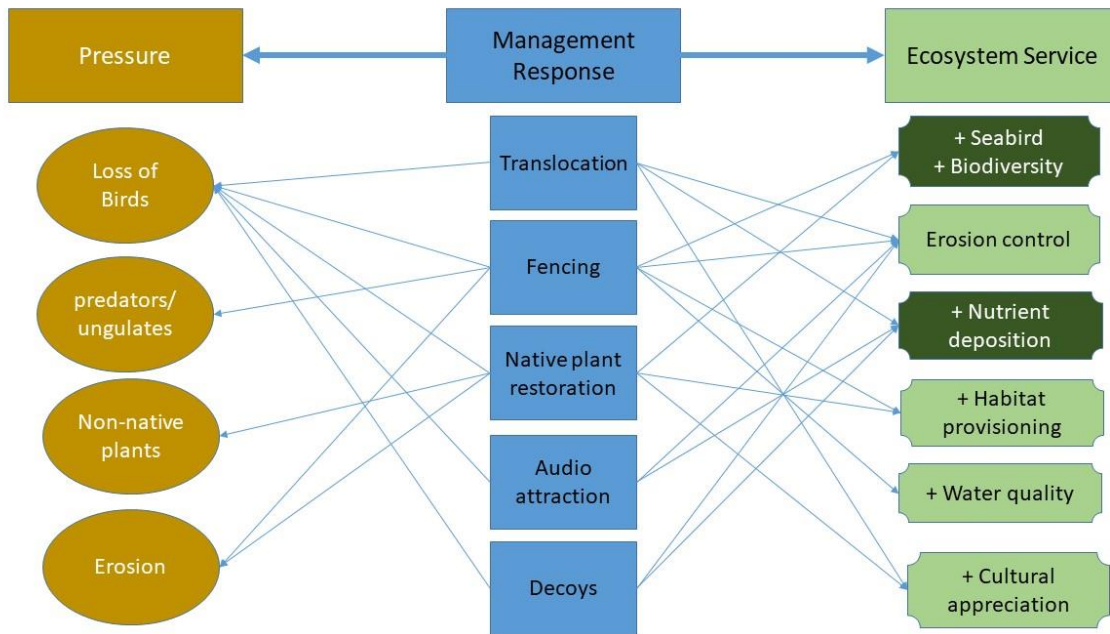


Figure 4.1 Conceptual diagram of management actions (blue) taken to address pressures on seabird populations (brown) and the ecosystem services that may be impacted directly (darker green) and indirectly (lighter green).



Figure 4.2. Endangered Newell's Shearwater chick (a), and endemic plant Koli'i, *Trematolobeilia kauaiensis*



Figure 4.3. (a) Predator-proof fence at Ka‘ena Point, O‘ahu, HI, and (b) ungulate-proof fence in Upper Limahuli, Kaua‘i, HI.

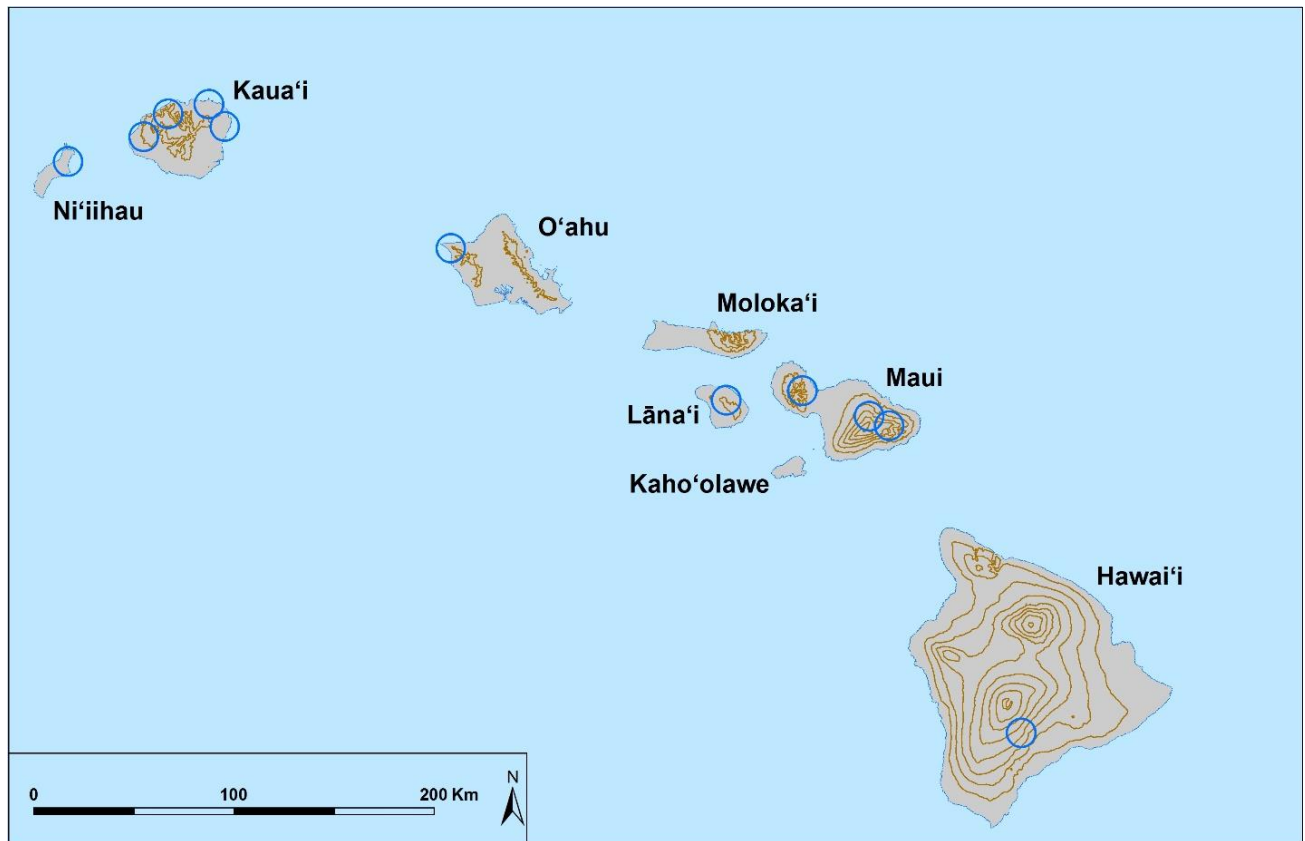


Figure 4.4. Map of the main Hawaiian Islands indicating sites of the surveyed projects. Map produced by Dr. J. Price, University of Hawaii at Hilo.



Figure 4.5 Song meter deployed in Upper Limahule Preserve, used to monitor for seabirds calling as an indicator of breeding presence.



## CHAPTER 5. SYNOPSIS

The goal of this dissertation was to gain a better understanding of how seabird losses impact ecosystems. Understanding how seabirds may have influenced native ecosystems in the past provides insight into how they impact ecosystems where they breed currently and what has been lost in ecosystems where they no longer breed. Understanding the past, as well as the current influence informs seabird restoration as well as native ecosystem restoration in Hawai'i and other seabird nesting areas worldwide. A better understanding both of the costs and the ecosystem wide benefits that are realized with restoration actions gives land managers better insight into seabird restoration actions and benefits.

With the dearth of precise information, the goal in Chapter 2 was provide broad estimates to better understand the conditions under which past native Hawaiian ecosystems may have evolved, avoiding the false precision that would result from a poorly informed statistical model. To understand how seabirds may have impacted Hawai'i in the past, I modeled the potential N deposition by seabirds in the pre-human past. Potential predators would have included a land crab (*Geograpsus spp.*) and a Hawaiian eagle of the *Haliaeetus* genus (Paulay and Starmer 2011, Hailer et al. 2015). Using published information from sub-fossil evidence as well as written accounts, I compiled a list of pelagic seabirds that could have nested on the main Hawaiian Islands in the time before human contact. I estimated three to four orders of magnitude decrease in N deposition to terrestrial ecosystems by seabirds since the arrival of humans. Though my model is coarse, there is little doubt that globally and locally, seabirds in the past contributed vastly more marine derived nutrients than they do today.

For millennia, seabirds nesting across Hawai'i fertilized terrestrial ecosystems with their nutrient rich guano. However, seabird populations have decreased drastically, and many seabirds



have been pushed into sub-optimal nesting habitat today. Seabirds currently nest at very low densities in montane ecosystems. Upper Limahuli and Pihea are two of the most densely populated areas with Newell's Shearwater and Hawaiian Petrel in Hawaii, with  $\sim 0.04$  burrows  $m^{-2}$ . Even in these low numbers, seabirds were still having an impact on the environment where they nest. Ammonium was higher in the soil in the seabird areas and the two dominant plant species contained marine-derived N in their foliage. Specifically, in the seabird plots, 32%, 28%, and 17% of the N in the soil and foliage of *M. polymorpha*, and *D. linearis*, respectively, came from a marine source. Contrary to my original hypothesis, I did not detect differences in the plant community composition between seabird and non-seabird areas despite the differences observed in soil nutrient availability. This may be because the seabird and non-seabird areas were located in remote areas with many similarities, little opportunity for recruitment of non-native seeds, as well as active weed suppression programs. Thus, with the legacy of seabirds potentially in both areas and the remote location of the sites, the addition of the marine nutrients did not alter the plant species composition. Future research could look at other colony sites in different environments, lower elevation, and sites that have been recently (10–15 yr) abandoned as nesting sites by montane nesting seabirds to see how the plant uptake of N varies and if there are more noticeable plant community composition differences. Knowing that seabirds in their reduced population numbers are still influencing native ecosystems makes the imperative to restore their breeding sites more compelling.

Due to the pressures facing seabirds and seabirds' life history, restoration is a long-term commitment. A thorough assessment of costs, benefits, and threats can produce more biological gain for a limited budget than restoration or conservation projects that do not conduct an economic assessment when designing a project (Naidoo et al. 2006). I worked with 12 seabird

restoration projects in the main Hawaiian Islands to conduct an assessment of the costs and benefits of various actions. Since seabirds are long-lived with delayed maturity, most projects do not yet have information about the success of the restoration action on seabird productivity. Instead, I created a rubric to ask questions about how the restoration actions that projects implemented impacted selected ecosystem services. In doing so, I addressed erosion control, conservation of biodiversity, seedling recruitment, and habitat for native organisms. There were no noticeable patterns between the size of the projects, actions used and the benefits. The lack of differences may be due to the highly individual nature of each project as well as the small sample size. However, it may be informative to use the ecosystem service improvement rubric through time within one project. Such temporal comparison will give the managers a better understanding of how the entire ecosystem is responding to the management actions they have chosen. Future research could observe how the costs and benefits change over time. Tools developed here will be helpful in planning restoration projects, as well as determining how successful they are in meeting project objectives. These tools are applicable in any restoration project anywhere in the world.

Based upon the research findings presented here there are several obvious next steps. First, there is a need to track seabird restoration projects into the future. Most of the projects discussed in Chapter 4 are ongoing and several new projects have been initiated incorporating active seabird restoration techniques. Following these new projects as well as the sites that I studied in Chapter 3 to track nutrient deposition could provide powerful insights into the dynamic relationship between seabirds and the terrestrial ecosystems where they breed. Second, as seabird populations increase how is this reflected in the soil and plant use of N and other nutrients? This could give us insight into the ecosystem wide impacts of seabird restoration.

Other restoration work in historical seabird nesting colonies should consider using active as well as passive seabird restoration techniques to restore seabirds and ecosystem function.

My research highlights the importance of seabirds in the Hawaiian ecosystems by quantifying the role seabirds played in the past as ecosystem nutrient providers, then learning how seabirds are still impacting native ecosystem, though in a lesser capacity, and finally by focusing on the costs of restoration and the ecosystem service benefits that come along with seabird restoration actions. My findings provide a lesson for seabird restoration globally as many of the challenges faced by managers and threats faced by seabirds are the same in many other seabird nesting grounds throughout the world. The many threats and challenges to seabird restoration necessitate an interdisciplinary approach. Hence, the tools presented here can improve the understanding of how restoration efforts affect the host ecosystems and how that changes over time.

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## **APPENDIX 1. Survey for project managers, including consent form.**



### **Survey for the Economic Analysis of Seabird Mitigation Options**

**Julia Rowe, Ph. D. Candidate,**

**University of Hawai'i at Manoa, CTAHR/NREM**

I am conducting an economic analysis of restoration efforts for seabirds. The purpose of this survey is to quantify the costs and benefits of different restoration approaches. This is part of a larger effort project looking at the benefits seabirds provide to ecosystems and humans.

#### **Electronic consent:**

Your participation in this research study is voluntary. If you decide to participate in this study, you may withdraw at any time. The phone interview will take about 45 minutes. The survey questions will be about restoration actions concerning seabird that you have engaged in. Should you decide to participate, your information will be kept confidential. All data will be stored in a password protected electronic format. To help protect your confidentiality, the surveys will not contain information that will identify you personally. The results of the study will be used for scholarly purposes only and may be shared with University of Hawai'i representatives.

If you have any questions about your rights in this project, you can contact the University of Hawaii, Human Studies Program, by phone at (808) 956-5007 or by e-mail at [uhirb@hawaii.edu](mailto:uhirb@hawaii.edu).

If you have any questions about the research study, please contact:

Julia Rowe, Ph. D. Candidate, University of Hawai'i at Manoa: 808 557 9750,  
[JRowe88@hawaii.edu](mailto:JRowe88@hawaii.edu)

Dr. Kirsten Oleson, Assistant Professor, University of Hawai'i at Manoa: 808 956 8864,  
[koleson@hawaii.edu](mailto:koleson@hawaii.edu)

Clicking on the “agree” button below indicates that:

- You have read the above information
- You voluntarily agree to participate
- You are at least 18 years of age

If you do not wish to participate in the research study, please decline participation by clicking on the “disagree” button.

- ❖ Agree
- ❖ Disagree

If you agree to participate, I will set up a time for a Skype or telephone call. I am supplying you with the questions that I will be asking so that you can gather necessary data or information before we talk. Thank you for your time and thoughtful consideration. If you have multiple projects or sites that you are restoring, I will treat each site separately.

- 1) Name and location of project
- 2) Total number of acres involved
- 3) Partner organizations
- 4) In your seabird restoration work, have you used any of the following actions?
  - a) Predator removal
  - b) Fencing
  - c) Invasive plant removal
  - d) Native plant restoration
  - e) Translocation of chicks
  - f) Acoustic playback
  - g) Artificial burrows
  - h) Other \_\_\_\_\_
- 5) If you engage in predator removal, which predators are you removing?
  - a) Rats
  - b) Mongoose
  - c) Mice
  - d) Ants
  - e) Cats
  - f) Dogs
  - g) Other \_\_\_\_\_
- 6) For each predator you are working on removing, during our interview, I will ask questions concerning the quantity, descriptions and price of equipment, supplies, and staff hours (see Appendix 1).
- 7) If you are using fencing, what kind of fencing are you using? Descriptions and costs (Appendix 1).
- 8) If you are conducting invasive vegetation control, what types of vegetation are you removing? Again, for all of these I am looking for descriptions and cost (See Appendix 2).

- 9) If you are engaged in native plant restoration, what plants are you restoring (Appendix 2).
- 10) If you translocated chicks, how many chicks did you translocate? How many have survived (See Appendix 3)?
- 11) If you are conducting acoustic playback, are you noticing an increase in natural calling? How often are you using playbacks (Appendix 3)?
- 12) Are you using artificial burrows (Appendix3)?
- 13) Do you record fledging success or population numbers for the colonies that you work in? If so, what is your measure? How do you obtain this number?
- 14) Do you measure any other indicators, such as seedling recruitment, invertebrate growth, etc.?
- 15) For the following Ecosystem Services (ES), I will ask you rate on a scale of 0 – 4 (Table 1) the response of the ES to the restoration action.

Ecosystem Service	0	1	2	3	4
Erosion Control	no change	5% less erosion	25% less erosion	50% less erosion	>75% less erosion
Conservation of Biodiversity	no change	One new native species seen in area/current native spp. discontinue decline	more than one new native species seen in the area and current native species stabilize	one new native species established in the area and current species stable	more than one new native species establishes in the area and current native species increasing
Habitat for Native Birds	no change	Current native plant species increase <b>or</b> decrease in bird predation	current plant species increase <b>and</b> decrease in bird predation	new native plants established and current species well represented/decrease in predation	Increase in vegetation structure, over and understory and decrease in predation if applicable.
Seedling Recruitment	no change	5 % more seedlings than before treatment,	25% more than before treatment	50 % more seedlings than before treatment	>75% more seedlings than before treatment.



# Number: Evaluation measures: I realize that frequently, increased chick or adult survivorship cannot be attributed to any one action when multiple approaches are being employed, however, if you measured fledging rates or any other measure of survivorship please include this. If you have any opinions concerning how this breaks down across mitigation actions, please include those. If you measured any other variables of success, such as increased plant recruitment, increased plant biomass, etc. please feel free to include those as well.

Thank you so much for your time, I look forward to talking with you soon.